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SOIL WATER SALINITY VARIATIONS AND THEIR EFFECTS ON *SPARTINA ALTERNIFLORA*

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ABSTRACT

Soil water salinities at five intertidal elevations of two salt marshes, one on the bay side of Bolivar Peninsula and the other on the bay side of Galveston Island, Texas, were sampled during the summer of 1978. Samples were taken at high and low tides on Galveston Island and high, low, mid high, and mid low tides on Bolivar peninsula during daylight hours. Salinity values of the soil water were higher near mean high water than at lower and higher elevations and sometimes reached 59 ppt on Bolivar Peninsula and 99 ppt on Galveston Island. The high salinity apparently physiologically damaged and killed the dominant vegetation, *Spartina alterniflora,* at approximate mean high water. The result was complete loss of plants or stunted growth of *Spartina alterniflora* at the zone of high salinity. High soil water salinities appeared to be caused by evaporation between tidal cycles and to be related to elevation, distance from bay waters, and range of tide.

Accepted 2 March 1983

INTRODUCTION

Salt marshes dominated by *Spartina alterniflora* provide nursery and protective habitat for estuarine organisms, prevent and slow erosion, and are a source of detritus for the estuarine food chain (Gosselink, Odum, and Pope 1974). Therefore, creation of new marshes and stabilization of shorelines with *Spartina alterniflora* is highly desirable. However, during transplant studies of a dredged material site near Galveston, Texas, survival, reproductive tillering, biomass production, and height of *Spartina alterniflora* was much less in a zone near the mean high water (mhw) mark than at lower seaward elevations and at higher landward elevations (Webb *et al.* 1978). A similar unvegetated zone near mhw is common in natural marshes of the area and height and biomass of *Spartina alterniflora* generally decreases with increasing elevation (Webb *et al.* 1979). Open sandy areas entirely devoid of vegetation or with scattered stands of *Salicornia spp.* and *Distichlis spicata* also occur in the zone near mhw in South Atlantic salt marshes (Cooper 1969).

The short stunted plants at mhw in the Galveston area may be equivalent to short form *Spartina alterniflora,* which occurs landward of tall creek

bank *Spartina* of the Atlantic Coast (Cooper 1969). However, the tall *Spartina* of the Galveston area is not generally associated with creek banks. Height of Galveston area *Spartina* generally decreases gradually shoreward from the bay. Differences in height and growth of tall and short form *Spartina* have been attributed to nitrogen limitations or other environmental gradients such as aeration, soil drainage (Linthurst and Seneca 1981, Linthurst 1979, Mendelssohn and Seneca 1979), salinity (Penfound and Hathaway 1938, Adams 1963, Smart and Barko 1978), or interaction of tidal water movement, dissolved iron, and sulfide concentrations in marsh soils (King *et al.* 1982).

Soil tests at the Bolivar Peninsula experimental site (L. R. Hossner, personal comm.), salt crusts observed near mhw, and preliminary measurements of soil water salinity indicated that salinity might be a problem to *S. alterniflora* growth. Wave action, shoreline debris, and soil compaction did not appear to be significant factors preventing plant establishment. To determine if salinity was the reason for decreased plant growth near mhw, intertidal soil water salinity was monitored at 5 elevations in an artificial and a natural salt marsh. These data were compared to growth data available for *S. alterniflora* from four areas (Webb *et al.* 1978, 1979). Environmental variables also were measured and tide predictions extracted from publications (NOAA 1978a,b) to determine their relation to soil water salinity. The term soil water salinity as utilized in this report refers to salinity of free flowing subsurface water in the pore spaces, cracks, and crevices of the soil (Brady 1974).

METHODS

Sampling stations at five elevations, 30, 45, 52.5, 60, and 75 cm above mean sea level (msl), were established along each of four transects on a revegetated dredged material area on the bay side of Bolivar Peninsula (Webb *et al.* 1978) and along three transects on the West Bay shoreline of Galveston Island. Soil water samples were taken from 7.6-cm diameter polyvinyl chloride (pvc) pipes permanently inserted to 20- and 36-cm depths at each sampling station. Water flowed through 0.16-cm-diameter holes drilled in the lower 10 cm of pipes. Caps prevented evaporation. Water in pipes was extracted with suction tubes. Total solids present in soil water samples were determined by a temperature compensated refractometer and converted to the nearest 0.5 ppt.

Soil samples adjacent to pipes were taken with a coring device and divided into 0-20-cm and 20-36-cm depth sections. Percent soil moisture was determined by dividing the difference in dry and wet weight by the wet weight of the soil.

Soil water samples at Bolivar Peninsula were taken weekly May 1 through August 14, 1978 at low, mid-high, high, and mid-low tides during daylight hours. Soil samples were taken weekly from 20 June through 14 August at high and low tides during one diurnal period. Soil water samples and soil samples were taken at high and low tides on Galveston Island weekly from July 7 through August 14, 1978. Predicted heights of tides were taken from tide tables (NOAA 1978a). Precipitation on Bolivar Peninsula was sampled by catch bottles but climatological data for Galveston (NOAA 1978b) was generally the same and was utilized for correlation tests for both sites. Bay water salinity was measured at each sampling period. Elevations were determined from nearby benchmarks of the U. S. Army Corps of Engineers with an automatic level along transect lines.

Soil water salinity readings were tested statistically by analysis of variance with Statistical Analysis Systems (SAS) for differences in dates, elevations, and tides. Relationships of soil water

salinity values to elevation, precipitation, soil depth, tides, distances along transects, and bay water salinity were tested by correlation matrices to determine relationships of these factors to high soil water salinity.

SITE DIFFERENCES

Distances along each transect varied because of differences in slope between transects and areas. On Bolivar Peninsula distances between sampling stations varied from 5 m to 27 m while total lengths of transects were 46.2, 55.3, 53.0, and 51.2 m. On Galveston Island distances between sample stations varied from 0.6 to 11.4 m. Total lengths of transects were 28.6, 17.2, and 21.0 m.

Soil texture was different between the experimental marsh site on Bolivar Peninsula and the Galveston Island natural marsh. The soil on Bolivar Peninsula was sandy in texture to a depth of 107 cm. The sand content ranged from 88.4 to 98.9 percent while clay was usually less than 2 percent (Dodd *et al.* 1978). Galveston Island tidal flat range sites similar to the one sampled are classified as Follett variant fine sandy loam. The texture of the upper 56 cm soil depth on area near the Galveston Island Site was 81.7 percent sand, 14.9 percent silt, and 3.4 percent clay (USDA-Soil Conservation Service 1979). The mean daily tidal range in the area is 23 cm to 55 cm (Lankford and Rehkemper 1978).

RESULTS

SOIL WATER SALINITY VARIATIONS

Bolivar Peninsula soil water salinity was different (statistically significant at $P<0.001$) by elevations for both depths sampled (Table 1). Highest soil water salinities occurred at the 52.5-cm elevation. The next highest salinities occurred at the 45-cm and 60-cm elevations, respectively, while the 75-cm elevation was consistently much lower than the other elevations. The 30-cm elevation closely reflected the bay water salinities. Soil water salinities varied widely among dates.

Soil water salinities on Galveston Island were significantly different ($P<0.01$) by elevation (Table 2). In contrast to Bolivar Peninsula, the greatest soil water salinity on Galveston Island was at the 45-cm elevation rather than the 52.5-cm elevation. Salinity readings at the 52.5-, 60-, and 30-cm elevations also were high with average high readings of 89.1, 51.4, and 39.9 ppt, respectively. Soil water was never present at the 75-cm elevation.

PLANT GROWTH

During 1977 density and height of the new transplants (1976, 1977) of *S. alterniflora* at Bolivar Peninsula was least at the 43 cm elevation and generally increased at lower and higher elevations (Table 3). This trend for height continued through 1978, but, during 1979, height declined with increasing elevation. During 1978 and 1979 density and standing green biomass followed a similar pattern. However, belowground biomass was least at the 43- or 54-cm elevation in 1978 and 1979. At the three natural salt marsh sites (combined means) all measurements declined with increasing elevation above 31 cm. At the natural sites *S. alterniflora* was generally absent above 66 cm and no measurements were made.

TABLE 1

Mean soil water salinity in 20- and 36-cm deep pvc wells at 5 elevations on Bolivar Peninsula.

	Elevation[3] (cm)											
	30		45		52.5		60		75			
Date	0-20cm depth	0-36cm depth	0-20cm depth	0-36cm depth	0-20cm depth	0-36cm depth	0-20cm depth	0-36cm depth	0-20cm depth	0-36cm depth	Rain[4] (cm)	Tide[5] Range (cm)
5/01	26.5±0.0[1]	26.5±0.0[1]	-[2]	51.3±5.5	-	59.4±10.7	-	37.9±11.8	-	-	T	33
5/10	29.2±0.0	29.2±0.0	-	-	-	-	-	-	-	-	T	12
5/19	27.9±0.1	27.7±0.2	-	37.7±4.1	-	38.2±3.1	-	21.1±0.5	-	-	0.0	33
5/23	27.0±0.0	26.9±0.3	-	38.1±7.9	-	-	-	-	-	-	0.0	18
5/25	26.2±0.2	26.0±0.2	30.8±3.1	31.6±1.9	54.3±0.3	58.5±0.9	-	-	-	-	0.0	18
5/31	25.9±0.0	27.3±0.3	-	27.5±8.1	-	-	-	-	-	-	T	30
6/08	19.7±0.3	21.2±0.7	27.2±1.6	30.5±1.9	42.1±5.5	34.2±2.1	25.9±5.4	28.7±3.5	-	13.1±1.1	8.1	12
6/16	22.2±0.2	22.0±0.2	26.5±1.5	31.7±2.2	42.1±7.0	45.1±11.6		-	-	-	0.8	36
6/20	23.3±1.6	24.0±0.4	24.8±0.5	32.9±2.2	45.0±3.5	41.8±2.5	27.9±1.6	29.3±3.7	-	-	0.0	54
6/27	25.7±0.4	25.1±0.5	-	-	-	-	-	-	-	-	0.0	27
7/06	26.1±0.4	27.3±0.4	-	-	-	-	-	-	-	-	0.0	15
7/11	27.4±0.9	28.7±0.9	-	-	-	-	-	-	-	-	0.0	21
7/17	26.3±0.5	27.4±0.5	-	-	-	-	-	-	-	-	2.0	54
7/26	28.9±0.4	26.3±0.5	42.0±8.4	40.1±8.4	47.3±12.7	47.9±6.6	-	27.2±3.0	-	-	4.8	33
7/31	28.4±0.6	25.8±0.2	40.8±7.1	44.8±7.9	27.0± -	46.4±12.2	-	-	-	-	2.8	39
8/08	24.5±1.0	29.2±0.9	40.8±5.9	44.6±5.9	45.9±6.5	44.6±4.6	23.4±2.9	27.9±2.4	13.6±2.1	10.6±0.5	T	21
8/14	31.4±0.2	31.4±0.4	-	34.6± -	-	-	-	-	-	-	0.0	48
Avg	25.8±0.3	26.4±0.2	31.5±1.4	36.1±1.4	44.7±2.6	43.7±1.9	25.7±1.6	29.0±1.8	13.6±2.1	11.6±0.6		

[1]Standard error of mean; N=4, N=8 or N=12 depending on tidal cycles.
[2]Measurements could not be made because of low water in pipes.
[3]Elevations were significantly different ($P<0.001$) at both depths in soil water salinity as tested by Analysis of Variance F-test.
[4]Precipitation between sampling periods; T-trace.
[5]Difference between predicted high and low tides during sampling period.

TABLE 2

Salinity of soil water in 36-cm deep pipe wells placed at five elevations on Galveston Island.

	Elevations (cm)					Precip- itation	Tide
Date	30	45	52.5	60	75	(cm)	range(cm)
7/07	----[1]	----	----	----	----	----	33
7/12	----	----	----	----	----	0.9	21
7/21	39.9+3.7	98.6+12.3	89.1+18.9	----	----	3.8	48
7/24	38.7+2.9	86.9+15.2	70.2	----	----	2.2	27
8/03	37.8+1.4	----	----	----	----	3.7	36
8/09	22.8+2.3	67.2+9.3	61.0+9.2	51.4+8.1	----	T	24
8/16	----	----	----	----	----	0.0	54
avg	34.4+2.2	84.2+7.6	74.1+9.2	51.4+8.1	----		

[1]Water not available in pipes to measure.

SOIL WATER SALINITY INFLUENCES

Tide levels affected soil water salinity and soil moisture. Tide levels during the 1977 growing season at Bolivar Peninsula (Fig. 1) appeared to be higher than those recorded over a number of years. The mhw for the period 1 January to 31 August 1977 was 77 cm while the long-term average was 55 cm. Therefore, new transplants initically were inundated daily a longer percentage of time than they would normally have been subjected to on the basis of the long-term average.

Soil water salinity due to tide level was significantly different ($P<0.01$) at the 0-36-cm depth at Bolivar, but it was not significant at the 0-20-cm depth (Table 1). However, strong correlations (Table 4) indicated a close relationship between the two depths. Soil water salinity was often different between tides on the same date. Daily differences in soil water salinity due to tide levels are not presented but are represented as part of the standard error of the mean in Table 1.

At Galveston Island soil water salinity varied slightly due to tide levels (analysis of variance F-test significant at $P<0.15$). Salinity differences between high and low tides on the same date occurred as at Bolivar (data not shown but reflected in standard deviation of mean). The highest salinities, which were recorded on July 21, corresponded with a wide tidal range that is typical of spring tides (Table 2).

TABLE 3

Mean heights of *Spartina alterniflora* Fall 1977, 1978, 1979 at Bolivar Peninsula experimental marsh and three natural marshes (combined means).

			Elevation (cm)					
Measurement	Area	Year	20	31	43	54	66	75
	Bolivar	1977	139	145	76	81	96	76
Density	Bolivar	1978	206	---	236	---	156	---
(stem/m^2)	Bolivar	1979	192	489	194	107	27	---
	Natural	1978	313	---	338	---	35	0
	Natural	1979	330	588	474	34	4	0
	Bolivar	1977	143	120	89	98	105	94
Height	Bolivar	1978	96	---	44	---	57	---
(cm)	Bolivar	1979	124	111	60	45	34	---
	Natural	1978	56	---	30	---	26	---
	Natural	1979	93	94	56	28	29	---
Standing	Bolivar	1978	936	---	267	---	201	---
green	Bolivar	1979	816	982	413	188	53	---
biomass	Natural	1978	501	---	269	---	43	---
g/m^2	Natural	1979	712	1107	462	26	3	---
Below	Bolivar	1978	861	---	182	---	451	---
ground	Bolivar	1979	1535	1652	1105	960	1157	---
biomass	Natural	1978	2364	---	3103	---	1145	---
g/m^2	Natural	1979	2867	5276	1932	1683	1429	---

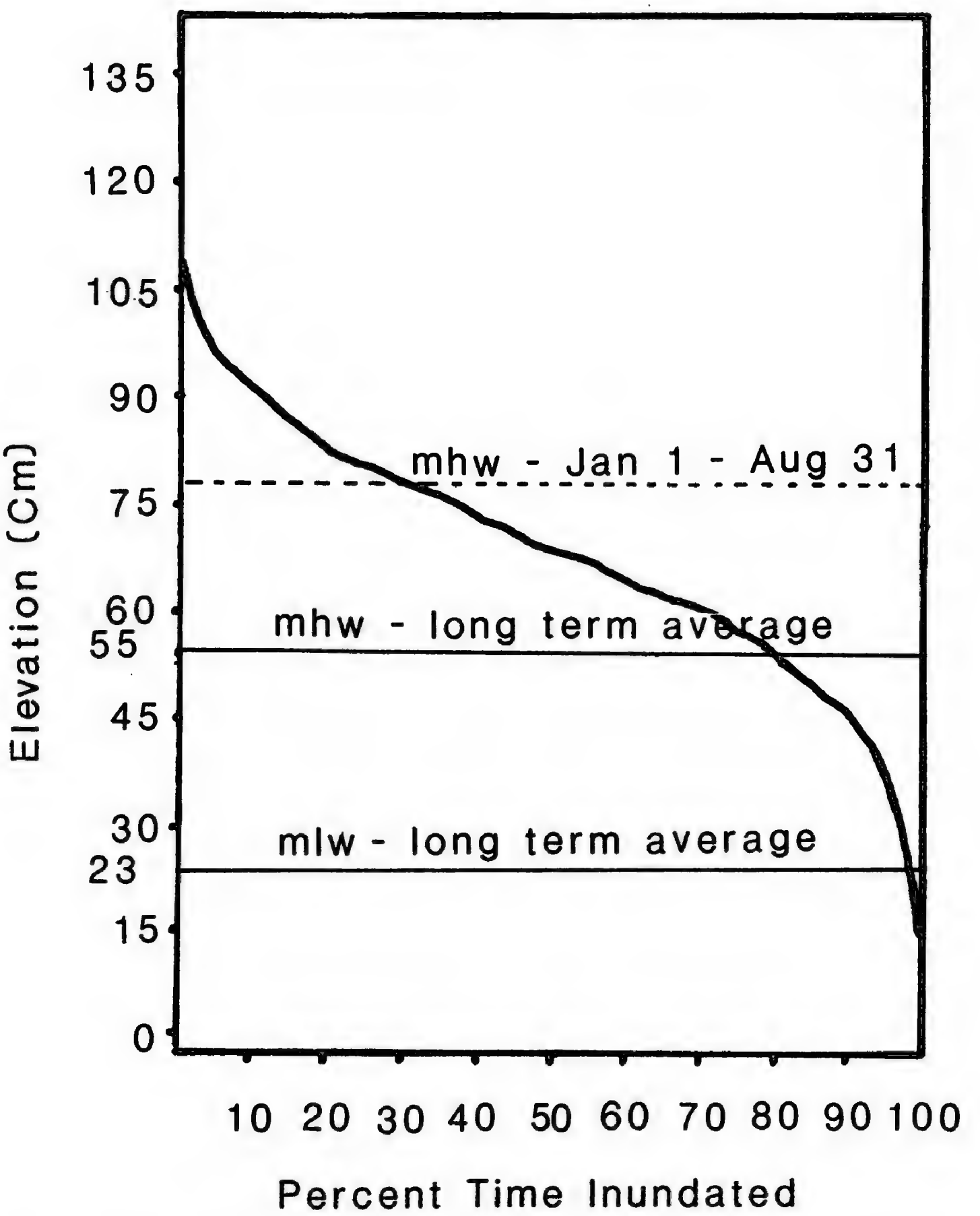

FIG. 1. Percent of time of inundation of Bolivar site at each elevation from January 1 to August 31, 1977. The mean for high and low water is also presented.

Soil moisture appeared to influence soil water salinity negatively as indicated by negative but strong correlations between soil moisture at the 0-20-cm depth and soil water salinities at Bolivar (Table 4). At Galveston Island soil moisture was generally the same for all elevations, except the 30 and 75-

TABLE 4

Correlation coefficients for water salinity, soil moisture, distance, elevation, precipitation, and tides for samples taken on Bolivar Peninsula in summer 1978.

Measurement	Transect Distance	Elev	precip.	SW sal. 0-20 cm	SW sal. 0-36 cm	Tides
Soil water sal. 0-20 cm	+0.24	+0.19	-0.03	+1.00	+0.85	+0.03
Soil water sal., 20-36 cm	+0.13	+0.13	-0.08	+0.85	+1.00	-0.07
Soil moisture 0-20 cm	-0.26	-0.33	+0.31	-0.41	-0.49	-0.15
Soil moisture 20-36 cm	-0.12	-0.14-	+0.35	-0.29	-0.27	-0.07
Bay water salinity			+0.56			

cm elevations. Soil moisture at the 0-20-cm depth was negatively correlated with distance along transects ($R = -0.56$) and elevation ($R = -0.56$). Soil moisture at the 20-36-cm depth was not as strongly correlated as the 0-20-cm depth.

Precipitation often affects bay water salinity (Bobb and Boland 1970) but precipitation was poorly correlated with soil water salinity (Table 5). However, examination of data indicated that precipitation caused drops in soil water salinity (Table 1). For example, salinity readings were generally lower on June 8 after 8 cm of precipitation than at other sample dates preceded by little or no precipitation (Table 1). Correlation tests indicated a relationship of soil water salinity with bay water salinity ($R = 0.56$) at Bolivar.

DISCUSSION

Spartina alterniflora is generally tolerant of normal estuarine water salinities and may achieve its best growth at 10 ppt (Linthurst and Seneca 1981), but salinities greater than 45 ppt cause dieback (Woodhouse *et al.*

TABLE 5

Correlation coefficients for soil water salinity, soil moisture, distance, elevation, precipitation, and tides for samples taken on Galveston Island, summer 1978.

	Transect			SW sal.	
Measurement	Distance	Elev	Precip.	0-36 cm	Tides
SW sal.					
0-36 cm	+0.74	+0.56	+0.25	+1.00	-0.11
Soil moist.					
0-20 cm	-0.56	-0.56	+0.14	-0.68	+0.04
Soil moist.					
20-36 cm	-0.41	-0.36	-0.03	-0.60	+0.08

1974) while concentrations of 50 ppt cause death (Shiflet 1963). Such high salinities have been recorded in salt marshes. Woodhouse *et al.* (1974) recorded soilwater salinities up to 110 ppt at higher intertidal elevations in two artificially established marshes. Surface salinity buildups resulted in salt damage, particularly to seedlings and young transplants. Apparently high salinities occurred when southeasterly winds caused extended periods of low water that coincided with periods of warm, clear weather. Teal (1962) reported 70 ppt salinity in *Spartina alterniflora* marshes and Rollins (1973) reported 116 ppt in a managed *Salicornia* marsh in California.

Soil water salinities above 45 ppt occurred only at the 45-cm to 60-cm elevations at either site. The hypersalinity of this zone probably resulted in the unvegetated area and stunted growth of plants at 43-cm to 66-cm at the natural salt marsh sites and at Bolivar Peninsula. However, some of the low biomass at the 75-cm elevation was probably associated with lack of soil moisture and absence of tidal inundation, which are necessary for *S. alterniflora* growth. The data in Table 3 seem to indicate that initially transplants responded differently at the 66- to 75-cm elevation range than when they became established. The same pattern of decreasing measurements with increasing elevation was present at all sites by 1979, except for belowground biomass. The differences in 1977 could have been related to the January to August 1977 tides that were higher than the normal yearly average. The long slope and sandy soil at Bolivar also may have resulted in some soil water percolation seaward from the upland, which may have influenced growth at the 66-cm and 75-cm elevations. The lack of an upward

slope above the natural sites would have prevented a similar situation at the natural salt marsh sites.

The narrow zone of hypersaline conditions found in this study probably limits the effects of the hypersalinity so that an entire marsh is not affected. Soil water levels were often below the zone of root growth; thus, harmful effects were limited to times of high soil water salinity concurrent with a high water table.

Apparently, salinity of the soil water was related to the alternate drying and wetting of the soil. The findings in this paper are in marked contrast to those of Taylor (1938) who reported that capillary action from the water table allows only minor fluctuations in salinity. Salt crusts were commonly observed on the surface of the soil. Salt crusts indicate that capillary action occurs with evaporation at low tides, thus concentrating salt at the sediment surface (Oppenheimer and Ward 1963). However, the salt crusts formed may not be important to plants until precipitation or tidal inundation brings the salt into solution.

The reasons for the exceptionally high salinities on certain days and differences in salinities between tides were not readily apparent. However, it appeared that salt in the soil increased with evaporation, which was affected by the height of tides and climatic conditions, such as temperature, humidity, and amount of wind. Unfortunately, the climatic conditions were not recorded to examine their effect. The importance of evaporation has been suggested before. Penfound and Hathaway (1938) reported that surface evaporation and transpiration play a part in increasing the salinity of the soil water.

According to Cooper (1969) salinity increases with distance from creeks and peaks near spring high tide in the short *Spartina alterniflora* zone and bare sand flats. Adams (1963) reported salinity values in excess of twice sea strength in salt flats. However, he found no significant differences between community types and neap or spring tides. Nestler (1977), Penfound and Hathaway (1938), and Hackney and de la Cruz (1978) also indicate that increases in free soil water salinity are closely related to distance from and elevation above flooding estuarine water. Soil water in marsh communities, as a rule, is decidedly more saline that the water of nearby lagoons, bayous, and lakes (Penfound and Hathaway 1938). Highest soil water salinities may occur when water levels are just below or above the marsh surface due to surface evaporation (Penfound and Hathaway 1938). Higher salinity of the water in the muddy foreshore of an estuary than the estuary water also was noted by Alexander, Southgate, and Bassendale (1932).

The effects of each environmental factor on soil moisture and salinity were not readily apparent from the correlation tests. Soil moisture apparently varied with precipitation, evaporation, surface and subsurface water drainage, and with tidal inundation. Soil moisture, in turn, probably affected salinity. Evaporation and transpiration, which would increase with wind, low humidity, high temperature, and low tides of extensive duration, certainly would have strong effects. The low salinities at the higher

elevations seem to indicate that tides do not influence soil water salinity above actual tidal reach. In other words, filtration of tidal waters landward through the sand was not occurring, which is in agreement with Lindberg and Hariss (1973), who reported that tides do not influence salinities above the high tide mark. On the other hand, salinities of the lower elevations indicated that frequent inundation prevented high salinity buildups. Flow of subsurface fresh water also may decrease the salinity of the soil water (Lindberg and Hariss 1973).

The different elevation and higher salinities on Galveston Island than on Bolivar Peninsula could have been associated with the higher clay and silt content in Galveston soils. Apparently, tidal waters do not penetrate the soil very rapidly. Reid (1930) reported that salinity of intertidal beach sand below 25 cm was not affected by alternating tides and a stream of fresh water passing over the sand as tides receded. Differences in tidal exchange due to topography, slope, distance along transects, and location also could be factors. The differences in slope and distance along transects, in particular, could have had significant influences. Nestler (1977) Cooper (1969), and Hackney and de la Cruz (1978) also have emphasized the importance of distance from estuarine water. Distance along transects at Galveston State Park was strongly correlated with soil water salinity but not on Bolivar. Slight errors in elevation determinations also must be considered because of local subsidence, which is very common in the area.

CONCLUSIONS

Salinity of the soil water that flowed into the wells at the 52.5-cm and 45-cm elevations on Bolivar Peninsula and at the 45-, 52.5-, and 60-cm elevations on Galveston Island was high enough on certain days to physiologically damage or kill *Spartina alterniflora* and *Spartina patens*. Lower growth measurements on plants at the 45-to 60-cm elevations than at the 30-cm elevation seem to indicate salinity effects. The exact reasons for the increase in soil water salinity on certain days are not known, but appear to be related to evaporation between high tides. Soil water salinity did not remain constant, but varied by tides and dates. Daily tidal fluctuations affected soil water salinity, but no consistent pattern of increasing or decreasing salinity with high or low tides was evident.

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TWO NEW NON-OCELLATE TRICHOCERCOUS CERCARIAE (DIGENEA: FELLODISTOMIDAE) FROM ESTUARINE BIVALVED MOLLUSCS IN GALVESTON BAY, TEXAS

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ABSTRACT

The sporocysts and non-ocellate trichocercous cercarial stages of two species of digenetic trematodes of the family Fellodistomidae are described from the gonad and digestive gland of estuarine bivalved molluscs in the Galveston Bay System, Texas. *Cercaria tageli* n.sp. develops in the stout razor clam *Tagelus plebeius* (Solander) and most nearly resembles *Cercaria laevicardium* (Martin, 1945). *Cercaria rangiae* n.sp. develops in the common rangia clam *Rangia cuneata* Gray and most nearly resembles *Cercaria chiltoni* Dollfus, 1925. The sporocysts of both species cause castration of their respective hosts.

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INTRODUCTION

Adult digenetic trematodes of the Family Fellodistomidae are intestinal parasites of marine fishes. Sporocysts and non-ocellate cercarial stages are known to develop only in bivalved molluscs and the metacercarial stages have been reported from a wide variety of invertebrates. The family is worldwide in distribution and contains a large number of genera and species.

The trichocercous fellodistomid larval forms were assigned by Dollfus (1964) to the Subfamily Steringophorinae, section II, containing the genera *Steringotrema, Bacciger* and *Lintonium. Steringotrema pagelli* has since been shown to have a bifurcate tail without a common stem (Koie 1980) and this generic grouping thus seemed no longer appropriate. Bray and Gibson (1980) revised the subfamilies of the Fellodistomidae, based primarily upon the morphology of the adult stages; they transferred *Stringotrema* to the Fellodistominae and placed *Bacciger* in the Baccigerinae *(Lintonium* was not treated). Koie (1980) employing the nomenclature of Bray and Gibson (1980), considered the life cycle types in the Fellodistomidae according to cercarial morphology and the type of molluscan host. Four natural groupings were realized as summarized in Table 1.

TABLE 1

Groupings of life cycle types according to cercarial morphology and type of molluscan host.

Life Cycle Group (Koie,1980)	Subfamily (Bray & Gibson 1980)	Cercarial Type	Molluscan Host
1	Fellodistominae & Monascinae	Furcocercous	Protobranch
2	Tergestinae	Furcocercous with flotation organ (Angel,1960)	Filibranch
3	Xenoperinae	Microcercous	Filibranch
4	Baccigerinae	Trichocercous cited as tricho-furcocercous in Koie, 1980	Eulamellibranch

Many non-ocellate trichocercous larvae which develop in eulamellibranchs and which may be ultimately included in the Baccigerinae are summarized in a tabular form by Holliman (1961). In addition, other apparently Baccigerine (Type 4 of Koie) larvae have been reported by Cable (1963), Chun and Lee (1976), Stunkard (1978) and Tang and Xu (1979, reported as an opecoelid).

Two new baccigerine larvae are reported in the present study from eulamellibranch bivalve molluscs whose morphology differs from that of the previously reported forms cited above.

MATERIALS AND METHODS

Host clams were collected from various localities in the lower Galveston Bay System and held individually in containers of filtered seawater at room temperature for a period of 24 hours. Water in the containers was then examined for the presence of larval Digenea. If results were negative, the water was changed and a second examination was made after a second 24-hour period. Following individual isolation in seawater, all molluscs were dissected and examined for the presence of larval Digenea.

The figures of the larval fellodistomids were prepared from measurements and drawings made from living specimens in seawater under light cover glass pressure. Additional information was obtained through the use of vital dyes and by the study of photomicrographs and prepared slides. All measurements given are in millimeters and were taken from living specimens during periods of relaxation under light cover glass pressure. Degrees of extension and contraction were also recorded. Measurements represent means and ranges taken from ten different specimens.

RESULTS

Cercaria tageli n.sp.

(Fig. 1a–d)

DIAGNOSIS: Trichocercous cercaria, body pyriform to oval, 0.15 to 0.21 long, by 0.12 wide posterior to ventral sucker. Tail 0.25 to 0.34 long by 0.038 wide, bearing 26 to 28 pairs of lateral finlets, (usually 27) each composed of six to seven rays in a narrow fan-like configuration oriented in a dorso-ventral plane and connected to each other by a membrane (Fig. 1d). Longest rays 0.125 in length. Oral sucker circular to oval, 0.036 in diameter, mouth ventral and subterminal. Ventral sucker 0.028 in diameter, slightly anterior to body midpoint. Pre-pharynx absent, pharynx 0.022 to 0.024 in length. Constriction of esophagus present just posterior to pharynx. Intestine bifurcating anterior to ventral sucker and crura extending just into posterior third of body. Gut contents staining red with neutral red stain. About eight pairs of penetration glands present but indistinct, staining light brown with neutral red, located laterally and slightly anteriorly to ventral sucker. Excretory bladder V-shaped, with arms extending anteriad past point of bifuraction of intestine. Bladder containing densely packed concretions. Caudal excretory duct extending through entire length of tail and opening posteriorly at tail tip. Concretions present throughout entire length. Main excretory tubules entering bladder on its anterior lateral margin, their lumina appearing ciliated, with ciliary beat resembling flickering of cilia of flame cells. Flame cell formula 2 [(3+3) + (3+3)] = 24. Anlagen of paired testes occurring laterally, midway between ventral sucker and posterior end of body. Outline of testes roughly circular, 0.018 in diameter. Ovary primordium medial, laterally oval, 0.019 by 0.012 and located posterior to testes in most specimens but appearing medial to, and also slightly anterior to testes in some specimens. Body tegument minutely spinose.

Cercariae swim tail first by lateral undulations of the tail stem. Cercariae swim to the surface, then remain motionless with tail twisted until as they drop slowly downward. No phototropisms observed.

Sporocysts (Fig. 1c) elongate, tapered anteriorly, up to 3.45 in length by 0.25 in width, pale orange-yellow, and each containing from 15 to 25 cercariae. Sporocysts occurring in region of gonad and digestive gland of host clam and causing parasitic castration. No visible effects on digestive gland observed. Cercariae emerging body first from terminal birth pore.

Sporocysts creeping actively when isolated on bottom of glass container.

HOST: *Tagelus plebeius* (Solander), stout razor clam

LOCALITY: Intertidal mud flats, southern portion of Galveston Bay, Texas

INCIDENCE OF INFECTION: 22 of 1804 clams (1.2%)

INFECTION EXPERIMENTS: (Ctenophores *(Mnemiopsis mccradyi),* grass shrimp *(Palaemonetes pugio)* and unidentified gammarid amphipods were exposed to the cercariae for two days and observed and/or dissected on various occasions up to two weeks after exposure, with negative results.

IDENTITY: This cercaria was compared to the previously reported

baccigerine larva cited in the introduction to this paper and is similar to the cercaria of *Bacciger bacciger* described by Palombi (1934) from venerid, donacid and pholadid clams in Italy; to the cercaria of *Lintonium vibex* (=*Cercaria laevicardium* Martin, 1945 and =*Cercaria laevicardii* Cable,

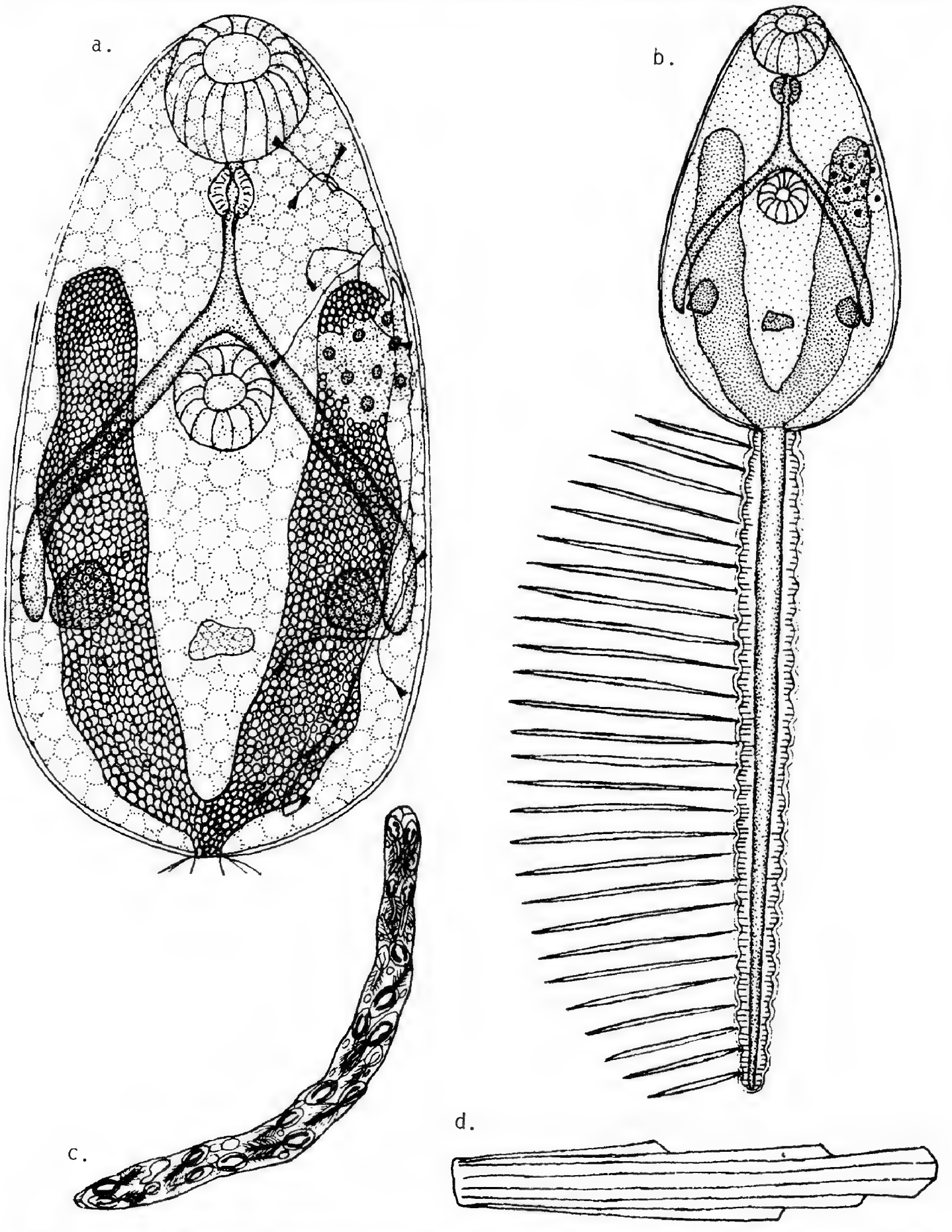

FIG. 1. Larval Stages of *Cercaria tageli* n.sp. *a.* Ventral view of cercarial body. *b.* Ventral view of entire cercaria. Penetration glands and details of excretory system omitted from right side. *c.* Sporocyst. *d.* Caudal finlet, view of transverse face.

1954) from the cockle *Laevicardium mortoni* in Massachusetts; to *Cercaria caribbea XXXIX* Cable, 1956 from *Tellina pauperata* in Puerto Rico; and to *Cercaria caribbea* LIII Cable, 1963 from *Tellina martinicensis* in Jamaica. Differences in the number and the arrangement of the penetration glands and in the structure of caudal finlets however preclude the present inclusion of *Cercaria tageli* in any of these previously described species.

ECOLOGY: *Cercaria tageli* was found from November through May in host clams collected from intertidal mud flats. Infected clams measured from 32 to 56 mm, and were thus large enough to have attained sexual maturity under normal circumstances (Wardle 1970). Palombi (1934) found that the cercariae of the closely related *Bacciger bacciger* (Rud.) escape the host clam and penetrate and encyst in the mud-dwelling corophiid amphipod *Erichthonius difformis.* When the amphipod is eaten by fishes of the genus *Atherina,* the encysted metacercariae develop into adults in the fishes' alimentary tracts. Martin (1945) described *Cercaria laevicardium* from the cockle *Laevicardium mortoni* in Massachusetts and found that the cercaria penetrates the ctenophore *Mnemiopsis leidyi.* Stunkard (1978) discovered that the hosts for the adult stage are puffer fishes of the genus *Sphaeroides* and that the adult worm had been previously described as *Lintonium vibex* (Linton, 1900) Stunkard and Nigrelli, 1930. Unencysted fellodistomid metacercariae were found during the present investigation in the ctenophores *Beroe ovata* Bosc and *Mnemiopsis mccradyi* Mayer from the southern part of Galveston Bay. Attempts to infect previously uninfected ctenophores of both species with C. *tageli,* however, were unsuccessful.

Cercaria rangiae n.sp.

(Fig. 2a–d)

DIAGNOSIS: Trichocercous cercaria, body 0.26 to 0.30 long by 0.14 at level of ventral sucker. Tail 0.40 to 0.45 long, 0.045 wide, bearing 21 pairs of lateral finlets each up to 0.12 in length and composed of six setae connected by a fine web (Fig. 2c). Setae arranged in dorso-ventral plane, their complexity not evident from dorsal or ventral view unless tail under great cover slip pressure. Oral sucker oval, 0.06 wide and 0.053 long, mouth subterminal and ventral. Ventral sucker slightly anterior, circular, 0.054 in diameter. Prepharynx absent, pharynx 0.036 long, crura of gut relatively short, extending just past posterior margin of ventral sucker. Walls of intestine thick and staining red with neutral red stain. Five pairs of penetration glands occurring laterally between level of pharynx and ventral sucker, four pairs occurring medially between pharynx and ventral sucker, and two pairs occurring on posterior margin of ventral sucker, for a total of eleven pairs. Their ducts extending dorsad and anteriad, opening above mouth. Penetration glands not staining with neutral red. One pair of small glands occurring on posterio-lateral margin of body, their short ducts opening in that region also. Excretory bladder V-shaped and containing no concretions. Arms of bladder long and extending to level of posterior margin of pharynx. A series of longitudinal striations occurring at base of bladder in region of its

connection with anterior part of tail, converging posteriorly at body-tail junction. Caudal excretory duct extending through entire tail and opening at posterior tip. Lumina of excretory collecting tubules ciliated from junction

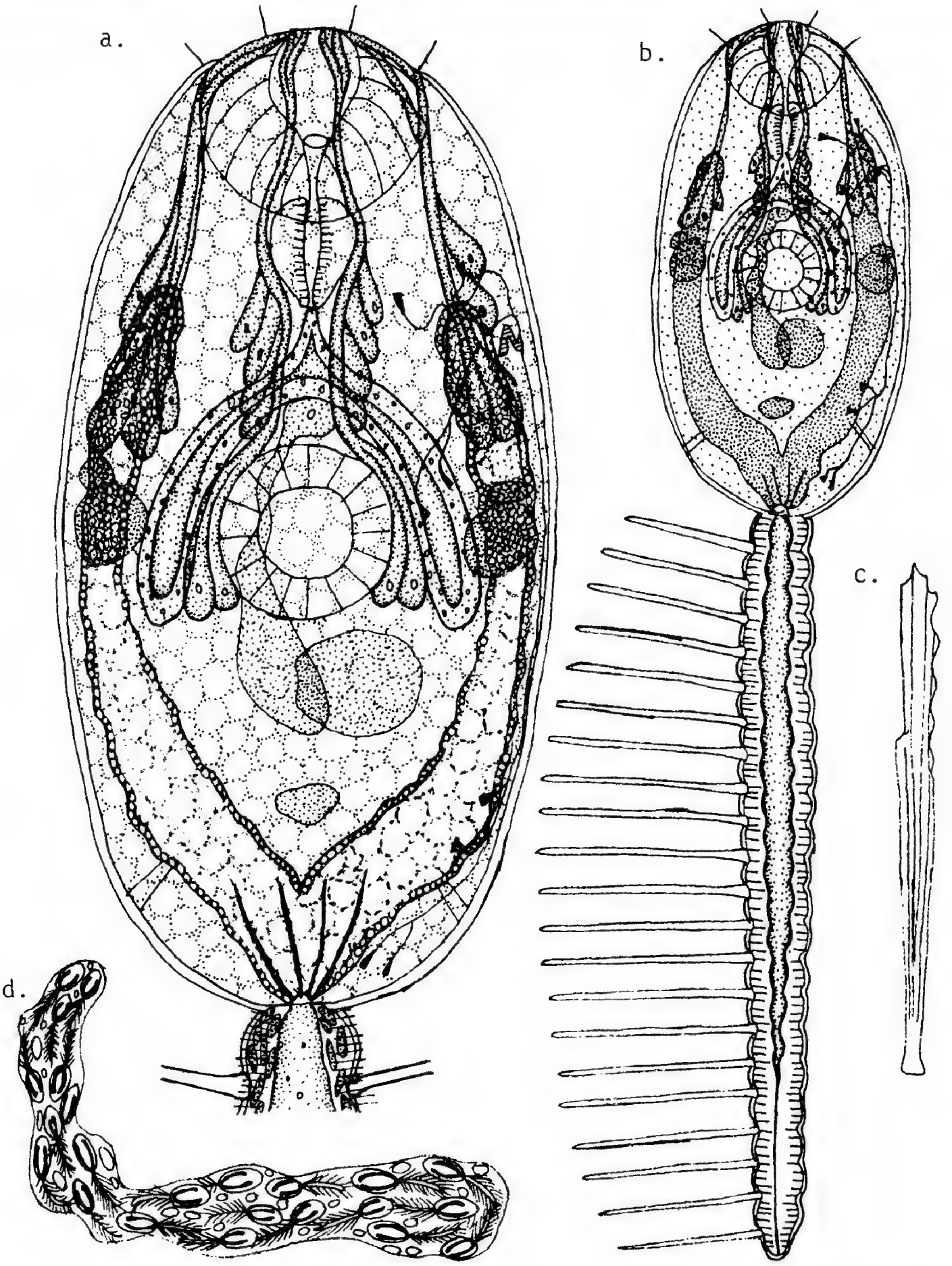

FIG. 2. Larval stages of *Cercaria rangiae* n.sp. *a.* Ventral view of cercarial body, and *b.* Ventral view of entire cercaria, details of excretory system omitted from right side. *c.* Caudal finlet, view of transverse face. *d.* Sporocyst.

of anterior and posterior tubules to connection of common tubule with arms of excretory bladder. Flame cell formula 2 [(2+2) + (2+2)] = 16. Anlagen of testes located laterally at level of ventral sucker, outline roughly circular, 0.28 in diameter. Ovary posterior to testes near posterior margin of ventral sucker and slightly to left of medial, roughly circular in outline, 0.32 in diameter. Cirrus sac arising at level of ovary, extending anteriad over the ventral sucker, and ending in medial pore anterior to ventral sucker. Body tegument minutely spinose, four prominent setae on anterior end, each 0.01 long. Tail bearing coarser spines between finlets (Fig. 2c), and coarser spines on posterior tip.

Cercaria swimming strongly, proceeding tail first to surface of water by lateral undulations of tail stem, then sinking slowly to bottom. No phototropisms observed.

Sporocysts (Fig. 2d) located in gonad and digestive gland of host clam; orange in color due to presence of orange globules embedded in tegument of sporocyst. Infected clams showing orange hue in visceral area, distinguishing them from non-infected clams appearing creamy white due to presence of normal gonadal material. Thousands of sporocysts occurring in most infections, each sporocyst containing up to twelve fully-formed cercariae and additional germ balls. Sporocysts 8.0 in length and 0.7 in width, widest point located near posterior tip. Individual sporocysts moving actively by creeping action of anterior portion. Birth pore terminal, cercariae emerging body-first from sporocyst.

HOST: *Rangia cuneata* (Gray), common rangia clam.

LOCALITY: Northern part of Galveston Bay in lower salinity subtidal waters in sand/silt bottom.

INCIDENCE OF INFECTION: 210 of 707 clams (29.7%). This species was compared to the previously reported baccigerine larvae cited in the introduction to this paper and was found to be unique in its lack of concretions in the excretory bladder (possibly attributable to its low salinity environment) and its relatively low number of caudal finlets (21, compared to 26 to 28 for most described species). *Cercaria chiltoni* Dollfus, 1925 described from *Chione suchtbergi* in New Zealand is similar in body form and has 21 to 24 pairs of caudal finlets and hence is probably the most closely related form to *Cercaria rangiae* which is presently known.

ECOLOGY: *Cercaria rangiae* was found year round, and persisted for up to sixty days in clams held in laboratory aquaria. Attempts to infect grass shrimp *(Palaemonetes pugio)* and gammarid amphipods with *Cercaria rangiae* yielded negative results. The host of the adult of this species is probably one of the species of fishes which can adapt to the low salinity and fresh waters of the northern parts of the Galveston Bay System.

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IXTOC-1 EFFECTS ON INTERTIDAL AND SUBTIDAL INFAUNA OF SOUTH TEXAS GULF BEACHES[1]

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ABSTRACT

A tar reef created by the IXTOC-1 oil spill in the Bay of Campeche was found in the intertidal region on Padre Island. This tar reef changed configuration from March to July of 1980 and had disappeared by October 1980. The tar in the reef was composed of greater than 20% oil by weight. The infaunal communities around this reef were affected by its presence when compared to prespill communities on Padre Island. The total number of organisms decreased and some fauna were completely excluded from the area of the reefs. For example, haustoriid amphipods were common on Padre Island before the spill, but were not observed in the area of the reef. Other species present before the spill had been displaced to areas immediately adjacent to the reef.

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INTRODUCTION

On 3 June 1979 the IXTOC-1 well in the Bay of Campeche, Gulf of Mexico, blew out and began spilling an estimated 30,000 bbl of oil per day into the surrounding waters. On 5 August 1979, IXTOC-1 oil slicks entered United States waters and within 1 week were washing ashore on south Texas beaches. The heaviest oiling along the Texas coast occurred between 18 and 29 August 1979. Before the well was capped on 23 March 1980, 140×10^6 bbl of oil had been spilled to create the largest documented marine oil spill. Approximately 3.3×10^6 bbl were stranded on the south Texas coast (Woods and Hannah 1981). Details of the well blowout and subsequent events are available in the Oil Spill Intelligence Report (1980).

The IXTOC-1 oil which entered Texas waters was a thick, viscous, oil-and-water emulsion referred to as mousse (Atwood and Ferguson 1982). No attempt was made to remove this oil which washed ashore along Padre Island beaches, except from areas of high recreational use (R. G. Whistler, Padre Island National Seashore, personal communication). By September

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1979, the IXTOC-1 mousse had mixed with sand and shell fragments in the intertidal and subtidal regions of Padre Island and formed asphalt-like tar reefs. By mid-winter (February), the reefs were still intact and showed little sign of deterioration. When this study was initiated in March 1980, scattered tar reefs remained on south Texas beaches. Our observations were corroborated by Gundlach, Finkelstein and Sadd (1981) who further reported a 7.7% oil content of these reefs.

Two studies done prior to the IXTOC-1 spill (Hill and Hunter 1976, Shelton and Roberson 1981) describe the distribution of Texas Gulf beach intertidal organisms. Thebeau, Tunnell, Dokken and Kindinger (1981) compared beach infauna one month before and one month after IXTOC-1 oil washed ashore on south Texas beaches, but did not discuss the Padre Island tar reefs. The persistence of the tar reefs provided an opportunity to study the long-term effects of these oil accumulations on beach infaunal communities. Combined with the short-term effects observed by others, this study provides information on the persistence of oil in the marine environment.

METHODS

The tar reef area studied was located 8.3 km north of the Mansfield Pass channel on Padre Island (26°38′29″ N, 97°18′05″ W). The site sampled was typical of south Texas barrier island Gulf beaches as described by Hill and Hunter (1976), with the exception of the tar reef. The beach is composed of relatively fine grain sized sediments (2.5 – 3.0 Φ) and is gently sloping (<2°–5°). The shore is microtidal with a diel range less than 51.8 cm at Port Aransas. Breaking waves are normally less than 1.0 m high. The study area corresponded to transect 5 of Thebeau *et al.* (1981).

Investigations were made on 5 March, 17 July and 23 October 1980. General observations on the configuration and nature of the tar reef were made. Stations were established on a transect traversing the tar reef from the high intertidal through the shallow subtidal area. Stations were located in the bar (ridges) and trough (low areas between ridges) system as follows (see Fig. 1): the most offshore Station (1) was located on the second bar; Station 2, within the second trough; and Station 3 on the first bar. The tar reef, which was situated in the first trough, was the site of 3 stations—Station 4 in the middle of the reef, Station OR on the offshore side of the reef, and Station IR on the inshore side of the reef. Station 5 was located at the water's edge at low tide and Station 6, at the water's edge at high tide. During low tide, samples were collected from all stations. All stations, except 1 and 2, were collected again at high tide. Samples were taken during daylight hours. Water temperature and salinity, wind conditions, and wave height were recorded along with the water depth at each station.

Triplicate 20-cm deep by 7.5-cm diameter cores were taken at each station. The cores were sectioned at 5-cm, 10-cm and 20-cm sediment depth and each section was preserved in 10% formalin containing rose bengal as a vital stain. In the laboratory, the sections were sieved through a 0.5-mm mesh screen and the remains examined for fauna. Organisms were identified to species or lowest possible taxon and counted.

The oil content of the sediments from each section of one of the replicate cores was determined for each station in March and July. The oil was extracted from the sediment using approximately 100 to 200 ml of reagent grade toluene. The toluene was then allowed to evaporate and the weight of the oil determined. Oil content was expressed as a percentage of the weight of the sediment.

Additional samples were taken from the tar reef in July for aromatic hydrocarbon analysis. The oil was fractionated with silica gel column chromatography after extraction with benzene. The silica gel was eluted successively with two column volumes of hexane and then benzene to

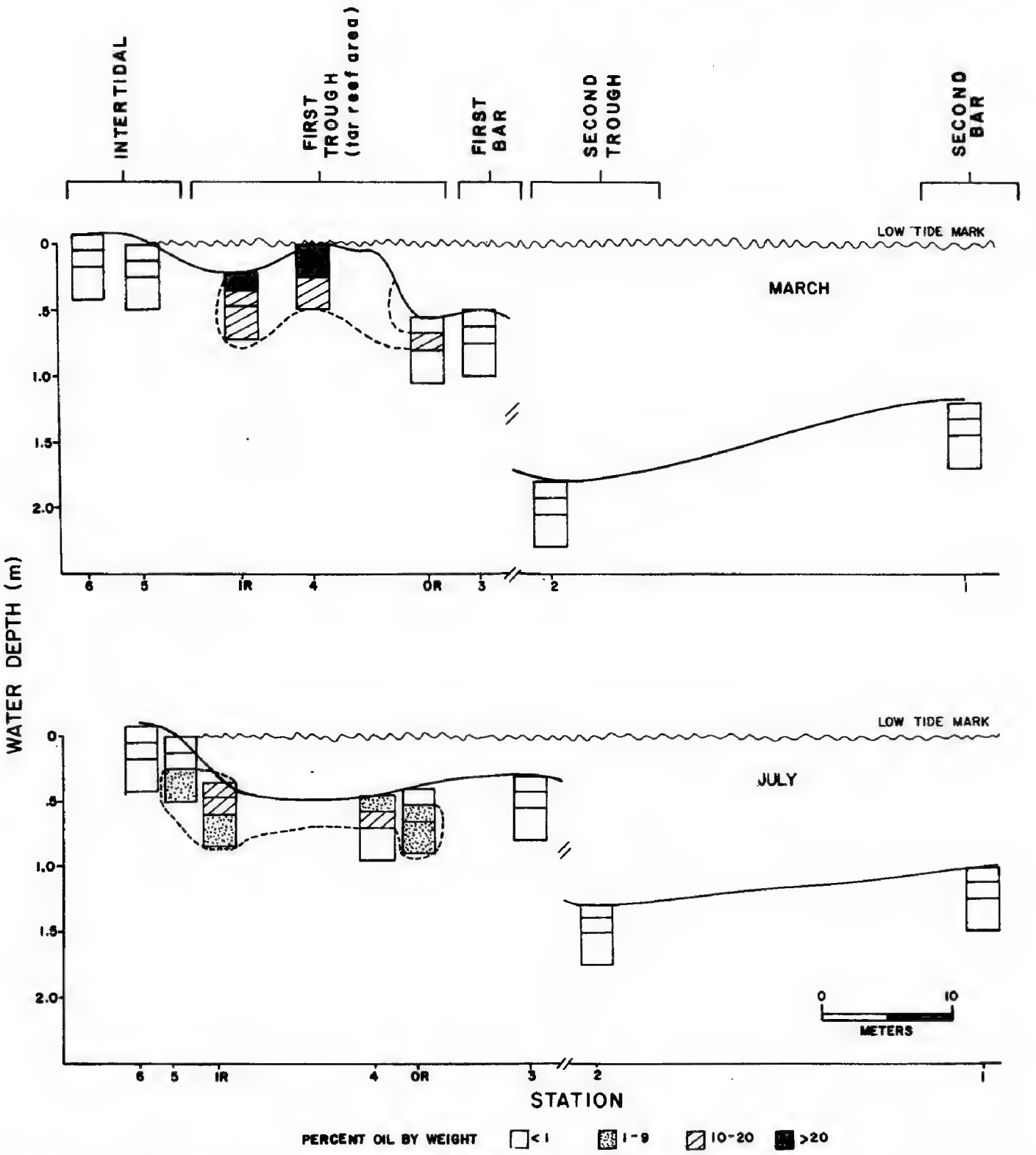

FIG. 1. March and July, 1980 beach profiles at the Padre Island tar reef transect as defined by water depth. Histograms indicate 5 cm, 10 cm, and 20 cm sections of cores taken at each station. Extent of the tar reef is determined from observations and oil content of sediment in each section of the cores and is outlined with a dashed line.

give the saturated and aromatic fractions, respectively. The aromatic fraction was then analyzed on a Perkin-Elmer 910 gas chromatograph. Electronic integration was performed with a Hewlett-Packard 3352B data system.

RESULTS

In March and July, 1980, there was a prominent tar reef located between the intertidal area (Stations 5 and 6) and the first bar (Station 3) as illustrated

in Figure 1. The tar reef appeared to be weathered, was mixed with a great deal of sand and shell, and looked like asphalt. The tar reef was more consolidated, contained more oil by weight in March than in July, and was not present in October, 1980.

In March the reef was approximately 122 m long and 6.5 m wide. The top of the reef (Station 4) was exposed at low tide and shallow troughs about 0.25 m deep had formed along the inshore (Station IR) and the offshore (Station OR) edges. The highest concéntrations of oil were found in the top 5 and 10 cm at stations IR and 4, respectively (Fig. 1). The bottom 15 and 10 cm of the cores at these stations contained 10 to 20% oil. Station OR samples indicated that the offshore edge of the reef was covered by 5 cm of sand.

Between March and July the reef changed from an elevated, unbroken structure that rose from the seafloor to an asphalt pavement flush with the surrounding sediment. The visible reef in July appeared to be sectioned into numerous finger-like projections that extended out from the water's edge at 45° angles. Also, the inshore and offshore troughs were no longer apparent and the crest of the reef was not exposed at low tide. The highest concentrations of oil were in the top 10 cm at Station IR and the second 5 cm at Station 4 (Fig. 1). The lowest concentrations of oil were found in the lower 10 cm of cores from Station 5 and IR and the lower 15 cm of sediment at Station OR. The reef was covered by 10 cm of sand at Station 5 and 5 cm of sand at Station OR. None of the July samples contained $> 20\%$ oil.

The oil from the reef was identified through gas chromatography as weathered IXTOC-1 oil (P. L. Parker, University of Texas Marine Science Laboratory, personal communication). The volatile, low molecular weight aromatics, while present in the benzene fraction of IXTOC-1 oil collected in July and August 1979 (Parker 1979), had disappeared from the oil collected on the reef in July 1980 (Figure 2).

The organisms found in association with the Padre Island tar reefs and their relative abundance in each of the sampling periods are listed in Table 1. The distribution of these organisms and the total number of species by station are shown in Figure 3. In March 74% of the animals and the greatest number of species were found at Stations 1 and 2. The most abundant organisms at these two stations were hesionid polychaetes. Species number and abundance were lowest at Stations 5 and 6 and no organisms were collected at Stations 3 and IR. *Petricola pholadiformis, Lumbrineris impatiens, Spiophanes* sp. and *Donax* spp. were collected in the tar reef area. The greatest number of animals in July were found at Stations 5 and 6 where *Scolelepis squamata* comprised 97% of the total abundance at Station 6 and 81% at Station 5. The densities were reduced to 50 organisms/m^2 at Stations IR and 4 then increased offshore to 150, 450, 800, and 1800 organisms/m^2 at Stations OR, 3, 2, and 1, respectively. The greatest number of species were found at Stations 2 and 3 and the fewest were found at Stations IR and 4. *Scolelepis squamata* and *Donax* spp. were the only animals collected on the reef and hesionids, *Ancinus depressus,* and *Donax* spp. were the most common species on the offshore side of the reef. In October 2700, 600 and

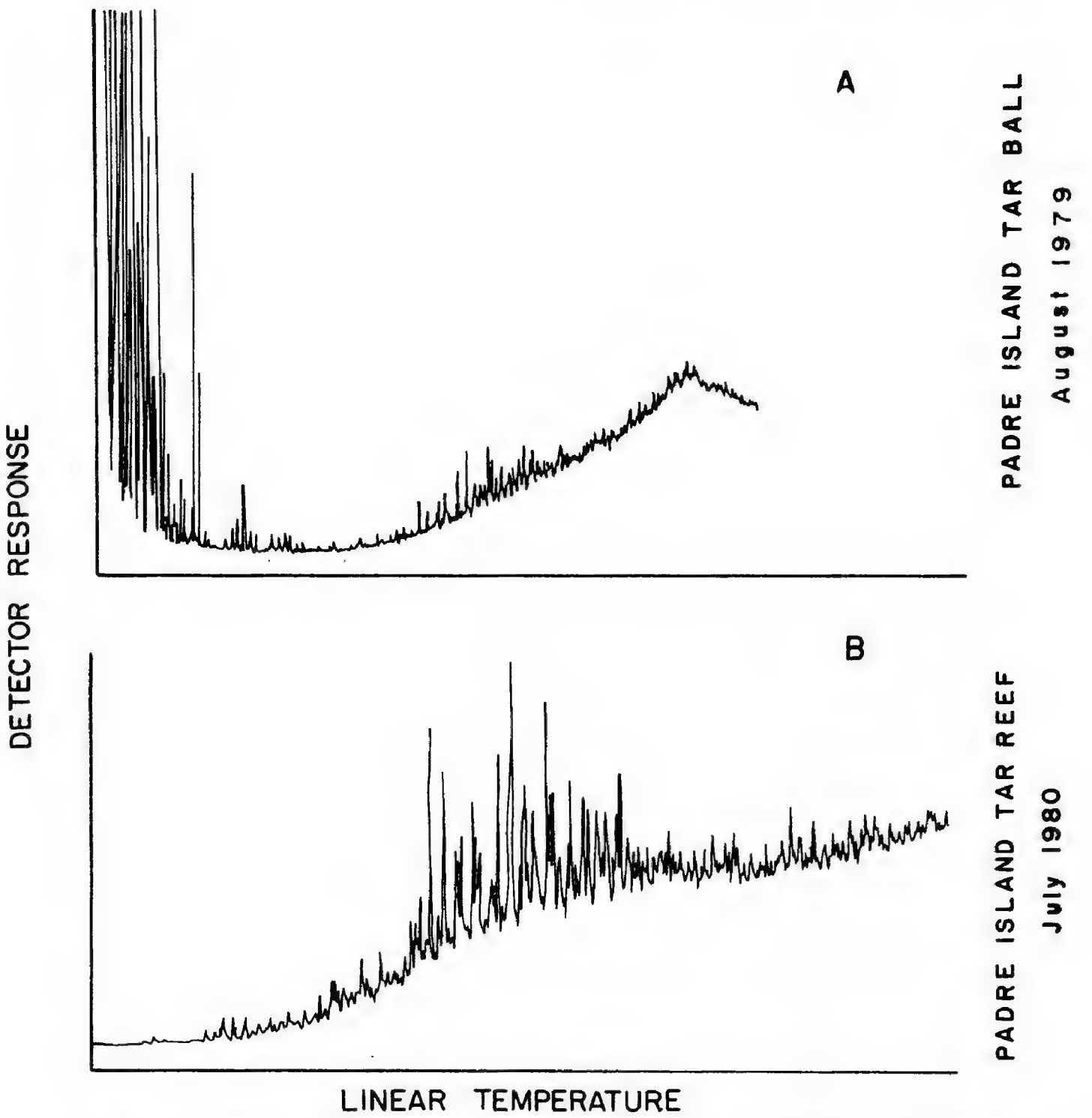

FIG. 2. Gas chromatogram of the aromatic (benzene) fraction of IXTOC-1 oil samples from South Padre Island tarballs in August 1979 (A) and the Padre Island tar reef in July 1980 (B). (A) taken from Parker 1979.

200 organisms/m^2 were found at Stations 6, 5, and 4 respectively. *Scolelepis squamata* was the only species found at Station 6 but it comprised 83% of the animals collected in October. Two species were collected at Station 5, and 1 was collected at Station 4. Stations IR, OR, 3, 2, and 1 were not collected in October.

Of the 17 taxa recorded, *Petricola pholadiformis* and *Spiophanes* sp. were the only two taken exclusively from the area of the tar reef (Stations 4, IR, and OR). The majority of the remaining animals were not found at these stations in great numbers. *Scolelepis squamata,* which comprised 72% of the total abundance at all stations, and *Donax* spp. were collected most often at Stations 6 and 5, respectively (Figure 4). Hesionids, the second most

TABLE 1

Species collected from all stations on Padre Island in March, July, and October 1980 and their relative abundances.

	Number of organisms/m^2		
	March	July	October
Phylum Mollusca			
Gastropoda (unidentified juvenile)			100
Donax spp.	100	450	
Petricola pholadiformis	200		
Phylum Annelida			
Pisionidens indica		150	
Hesionidae	501	1550	
Onuphis eremita		100	
Lumbrineris impatiens	250	200	100
Spionidae (unidentified juvenile)		100	
Scolelepis squamata	50	6400	2900
Spiophanes sp.	50		
Spiochaetopterus sp.	351		
Paraonis fulgens		200	
Owenia fusiformis	300		
Phylum Arthropoda			
Ancinus depressus	100	550	
Bowmaniella sp.		100	
Callianassa sp.			100
Emerita benedicti		50	400

abundant group increased from 50 organisms/m^2 at Station 3 to 180 organisms/m^2 at Station 1. *Lumbrineris impatiens* was found in large numbers only at Station 2.

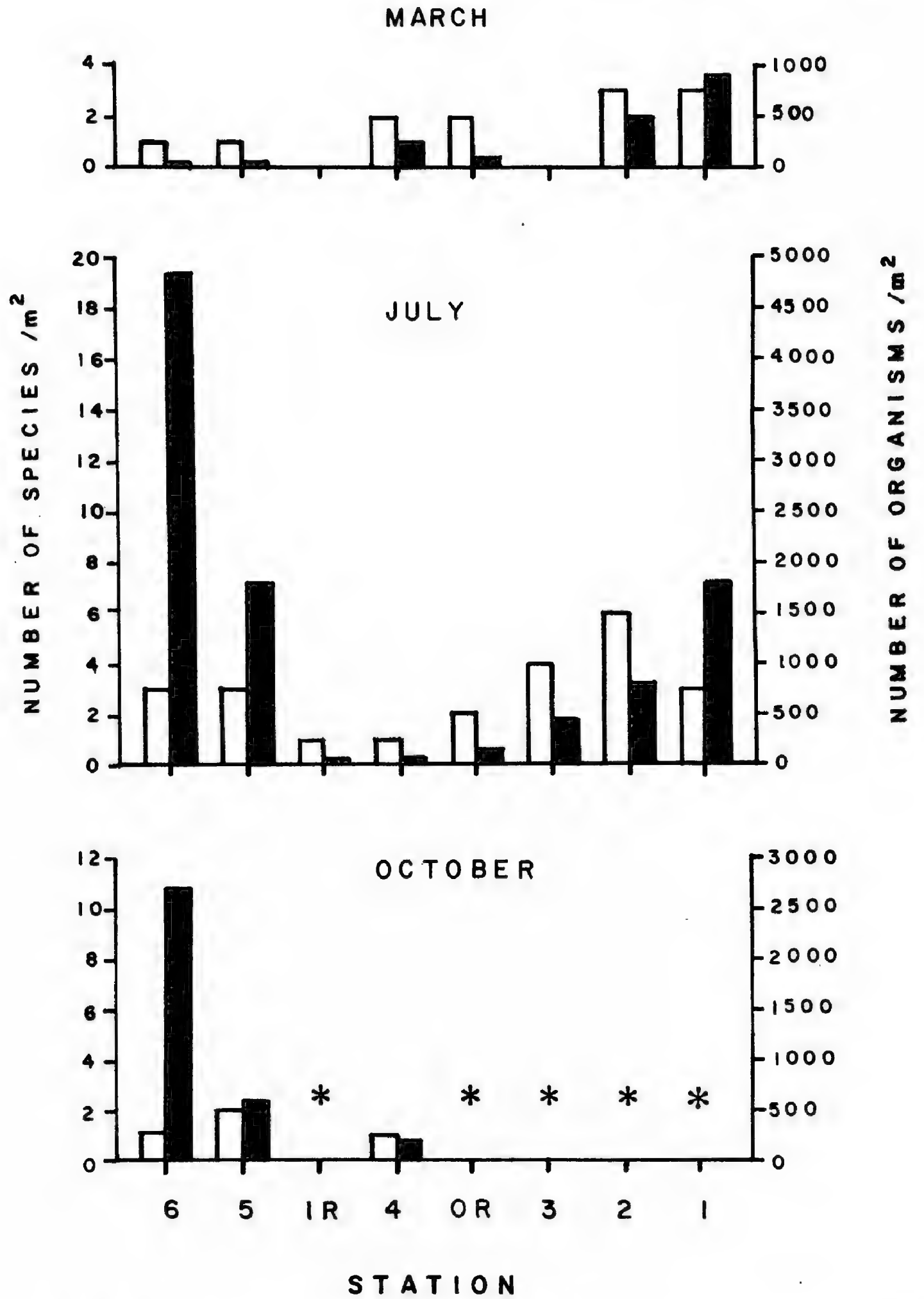

FIG. 3. Number of organisms/m² (shaded histograms) and number of species (open histograms) from all sections, replicates, and both tidal periods. Blanks indicate zero values and asterisks (*) indicate no samples taken.

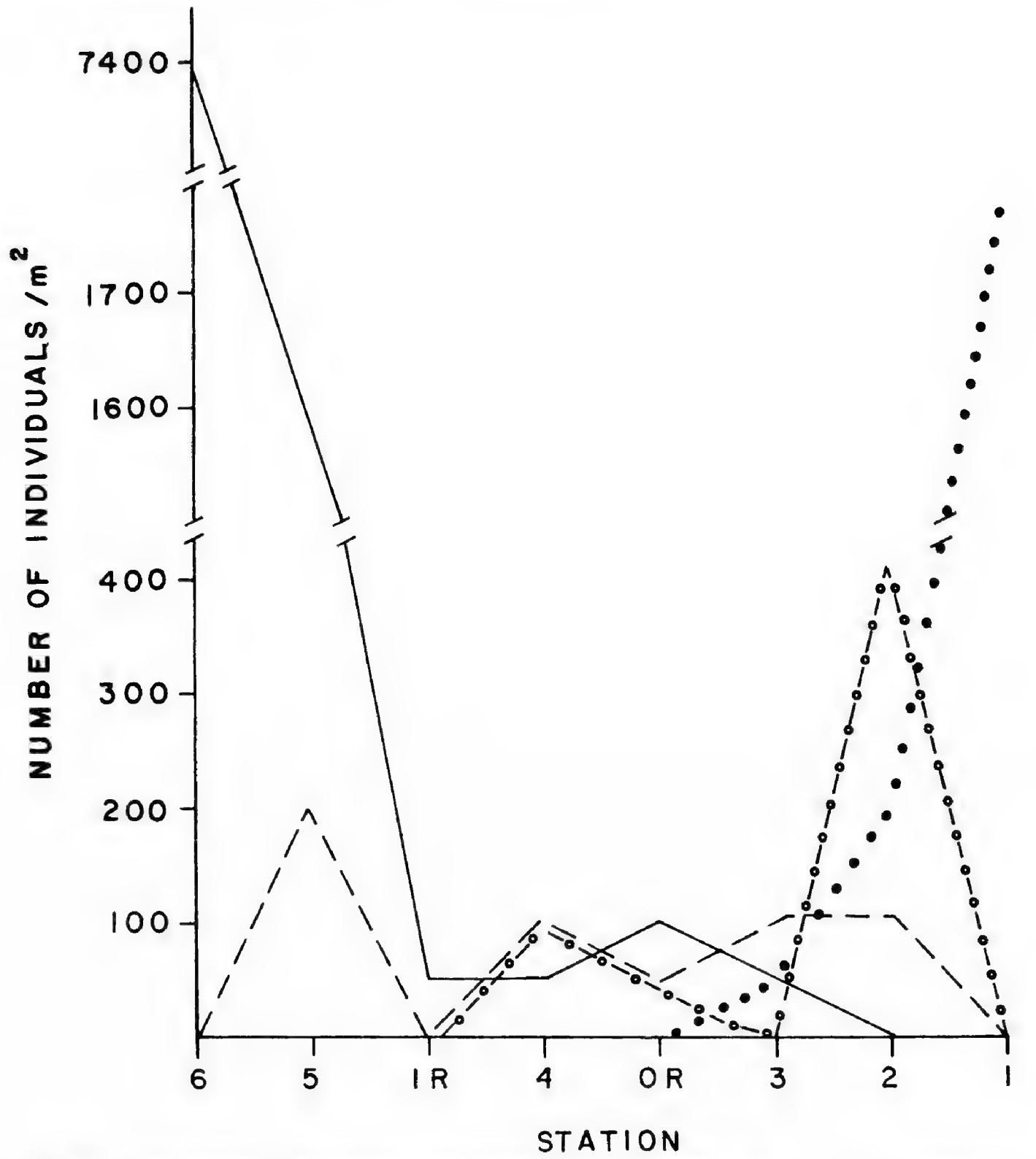

FIG. 4. Distribution of *Scolelepis squamata* ———, *Donax* spp. ----------, *Lumbrineris impatiens* -o-o-o-o-o, and Hesionidae ●●●●●● across the tar reef transect as indicated by the total individuals/m² for March, July, and October.

DISCUSSION

Factors influencing changes in the configuration, nature, and oil content of the tar reef are difficult to pinpoint. The differences observed between March and July could have been the result of changes in the tar reef itself, or the beach profile, or both.

According to Hill and Hunter (1976), in calm weather, as is common during summer months, the inner bar migrates shoreward and tongues of

sand are built from the bar into the inner trough. Certain characteristics of the July tar reef indicate that these changes in beach morphology may have given the impression that the reef itself had changed, when in fact, only the shoreline had changed.

The presence of oil buried below 10 cm of sand at Station 5 in July indicates that the shoreline had prograded and covered the inshore edge of the tar reef. Also, in March the highest concentration of oil was found at Station 4. In July the highest concentration of oil was found only a short distance from the water's edge at Station IR. This indicates that the first trough had been filled and a new first trough had formed farther seaward. The discontinuous finger-like projections of the tar reef in July give further evidence that the beach and not the tar reef had changed. It is possible that during the early summer of 1980 sand from offshore (the first bar) was deposited in the first trough and intertidal region of the beach. This would have covered the inshore edge of the tar reef and uncovered the offshore edge. Then, as Hill and Hunter (1976) described, tongues of sand were deposited on the newly uncovered offshore edge of the tar reef giving the impression that the reef had reformed into finger-like projections. Therefore, the reef visible in July may actually have been the offshore edge of the March reef.

Besides normal movements of sand which may have created the apparent differences in the tar reef configuration between March and July, catastrophic events may have caused the reef to be covered by large amounts of sand by the October sampling. In August 1980 Hurricane Allen struck the lower Texas coast. Gundlach, Finkelstein and Sadd (1981) found that many of the Padre Island tar reefs had survived Hurricane Allen and were intact in the intertidal region. This would indicate that the tar reef of this study had also survived the hurricane and had simply disappeared from sight. Amos, Rabalais and Scalan (1983) reported that storm waves from Hurricane Allen eroded the fore dunes and widened the beaches along the south Texas barrier island. The widening of the beaches was caused by sand that was eroded from the foredunes and deposited in the intertidal. If the Padre Island tar reef we studied had not been destroyed by Hurricane Allen it is possible that it was covered with sand and, in fact, may still exist. Tar reefs created by the *Arrow* spill persisted for 6 years in the intertidal region of Chedaducto Bay, Nova Scotia (Keizer, Ahern, Dale and Vandermeulen 1978). Gundlach, Berne, D'Ozouville and Topinka (1981) found asphalt reefs on sand and gravel beaches two years after the *Amoco Cadiz* spill.

As it is difficult to determine what caused the changes in the reef through time, it is also difficult to determine the reef's effect on the surrounding infaunal communities. Although the toxic effects of the oil could not be measured, comparisons of the chemical characteristics of the tar reef and other IXTOC-1 oil samples provide the basis for determining the possible effect of the tar reef on the beach communities. The oil samples taken from the reef in July show that low molecular weight aromatic hydrocarbons, which Jordan and Payne (1980) found to be the most toxic component of oil,

were absent. However, tar balls from South Padre Island collected in August 1979 (Fig. 2) and oil from the beach on Mustang Island in August 1979 indicated that the IXTOC-1 oil washing ashore in Texas contained these toxic compounds (Parker 1979). In fact, Rabalais, Arnold and Wohlschlag (1981) demonstrated that the IXTOC-1 oil collected on Mustang Island was very toxic to the eggs and larvae of red drum *(Sciaenops ocellatus).* Even though there were no toxic compounds present in July 1980, the possibility existed that these compounds were present in the oil when the tar reefs were formed.

Other possible ways the tar reefs could have affected the beach infaunal communities were demonstrated in the laboratory by Kalke, Duke and Flint (1982). In their study, the total abundance, biomass, species diversity, and equitability of *in situ* colonized laboratory communities decreased when exposed to oil from IXTOC-1 tar reefs. The authors proposed that, based on the oxygen content of the sediment, the presence of IXTOC-1 oil on the surface of the sediment reduced the habitat space available for infaunal organisms.

More evidence for the adverse effects of the tar reef on the beach infaunal communities can be found by comparing distributions of organisms on the tar reef to those normally found on south Texas Gulf barrier island beaches and to those found before and after the spill. The pre-spill and post-spill communities reported by Thebeau *et al.* (1981) along a portion of the beach near our study area and the communities from the Padre Island tar reef are compared in Table 2. Thebeau *et al.* (1981) reported a post-spill decrease in the number of organisms/m^2 at all stations in the intertidal, subtidal, and tar reef area. In our study the mean number of orgnisms/m^2 in the tar reef area had not recovered by July 1980 to the 1979 pre-spill numbers while intertidal and subtidal organisms were more numerous than in 1979.

Further evidence for the effect of IXTOC-1 tar reefs on the beach infaunal communities is found when comparisons to communities normally found on south Texas Gulf beaches are made. Haustoriid amphipods are among the most common intertidal and shallow subtidal Padre Island beach invertebrates according to Hill and Hunter (1976), Thebeau *et al.* (1981) and Shelton and Robertson (1981). These animals were also found to be common on Mustang Island, Texas during this same period (unpublished data). Haustoriid amphipods were not collected during our study. The susceptibility of amphipods to oil pollutants has been demonstrated. Lee, Welch and Nicol (1977) found that two amphipods, *Gammarus mucronatus* and *Amphithoe valida* were more sensitive to number 2 fuel oil and south Louisiana crude oil than two species of benthic polychaetes and one species of shrimp. McCauley (1966) reported that amphipods disappeared from oil polluted rivers in Massachusetts. The amphipod *Gammarus* sp. and the isopod *Idotea* sp. were also absent from the intertidal *Fucus* community after a spill as reported by Notini (1978), but these highly mobile crustacea were present 1 year later. In this case all remnants of the oil had been removed and no tar reefs formed. It is possible that haustoriid amphipods would also have been reestablished after one year if the Padre Island tar reefs had been removed.

TABLE 2

Comparison of Padre Island Gulf beach infaunal densities before the IXTOC-1 spill, August 1979, and after the spill, September 1979 and July 1980. One year post-spill densities shown are means of Stations 5 and 6 for the Intertidal Area Stations IR, 4 and OR for the Tar Reef Area, and Stations 1, 2, and 3, for the Subtidal Area.

	Infaunal Densitites (number of organisms/m^2)		
Time Period	Intertidal Area	Tar Reef Area	Subtidal Area
August 1979* (pre-spill)	957.3	243	632.7
September 1979* (post-spill)	171.3	177	338.0
July 1980 (one year post-spill)	3375.0	83.0	1016.0

*Numbers taken from Transect 5 of Thebeau et al. (1981): mean of Intertidal Area Stations 1, 2, and 3; Tar Reef Area Station 4; and mean of Subtidal Area Stations 5, 6, and 7.

Other beach species, although not excluded from the area of the tar reef, were found to be restricted to areas not covered by oil. *Lumbrineris impatiens,* which were found by Hill and Hunter (1976) to occur in large numbers in the first trough and first bar on Padre Island and intertidally on Mustang Island, Texas (unpublished data), were collected in large numbers only at Station 2. The most common beach inhabitants, *Scolelepis squamata* and *Donax* spp., were collected in the intertidal regions away from the tar reef. In another study Chasse (1978) also found that the polychaetes *Arenicola, Laonice,* and Opheliidae were resistant to oil from the *Amoco Cadiz* but haustroriid amphipods were "heavily to moderately" affected.

The tar reefs formed from the IXTOC-1 oil spill were a persistent feature along the intertidal region of Padre Island. Even though the reefs may have been covered by the dramatic events of Hurricane Allen, it is possible that they will some day resurface. As late as December 1980 remnants of the IXTOC-1 spill were uncovered by winter storms on Mustang Island (Amos 1983). A reduction in the numbers of organisms and the exclusion of some species from the area of the tar reef indicate that these reefs were affecting the intertidal communities. The potential toxic compounds present in the oil that formed the reef along with the physical presence of the reefs could explain their effect on the intertidal community and could contribute to a

renewed impact on the infaunal organisms if the reefs are ever uncovered. Even if these reefs are never reexposed it is possible that like the benthic fauna in Buzzards Bay, Massachusetts where species diversity remained low 3 years after the *Florida* oil spill (Sanders 1978), the benthic fauna on Padre Island will feel the impact of the IXTOC-1 tar reefs for many more years to come.

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OCCURRENCE AND DISTRIBUTION OF REPTANT DECAPOD CRUSTACEAN LARVAE IN NERITIC LOUISIANA WATERS: JULY 1976

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ABSTRACT

Oblique hauls of a 61 cm bongo sampler (0.505 mm mesh) at 33 stations yielded 66 kinds and at least 20 families of anomurans and brachyurans. Wet displacement plankton volumes (fishes removed) ranged from 4.8–88.0 ml with < 1.0 to 27.0% reptant larvae. *Callinectes* spp. and *Portunus* spp. were the only reptants occurring at all stations and were first and third, respectively, in overall abundance. First and second zoeal stages of *Callinectes* spp. were most abundant at nearshore stations; more advanced stages were predominant offshore. Larvae of fiddler crabs, *Uca* spp., were second in overall abundance but occurred at only 24 stations. Our data support patterns of megalopal and postlarval recruitment to estuarine areas by *Callinectes* spp., *Uca* spp., *Pagurus pollicaris* and *Clibanarius vittatus*.

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INTRODUCTION

Recent studies (Felder 1973; Powers 1977; Felder and Chaney 1979) have provided new information and summarized literature on adult reptants in the northwestern Gulf of Mexico; however, knowledge of early life history stages of these decapods remains sparse. Most studies of northern Gulf reptant larvae are of the "blue crab" (Darnell 1959; More 1969; King 1971; Atkins 1972; Perry 1975; Stuck and Perry 1981), although several researchers mention collecting reptant larvae during zooplankton surveys in Louisiana and Mississippi estuaries (Cuzon du Rest 1963; Gillespie 1971; Perry and Christmas 1973; Hawes and Perry 1978). Other northern Gulf estuarine studies have treated specific reptant larvae or the entire larval decapod fauna. Fotheringham and Bagnall (1976) studied seasonal abundance of larvae of four species of hermit crabs in Texas, and Shipp (1977) reported 12 genera of decapod larvae including *Uca* spp., which she found predominant, from a tributary of Mobile Bay, Alabama.

In neritic Gulf waters, two zooplankton studies reported "decapod zoeae" and "brachyuran megalopas and zoeas" (Ragan 1975; Berkowitz 1976). Hammer (1974) and Maris (1980) reported the distribution of scyllarid and

porcellanid larvae, respectively. In a neuston study of the Texas outer continental shelf Wormuth, Pequegnat and McEachran (1979) reported the capture of "77 decapod taxa including the different larval stages", but enumerated and briefly discussed only the most abundant kinds.

Perhaps the major reason for the lack of information on the distribution and abundance of larval decapods, particularly reptants, in the northern Gulf and elsewhere has been the lack of aids for their reliable identification (Sandifer 1973). Less than 15% of the crab species reported for the Gulf of Mexico by Powers (1977) have any of their larval stages described. Literature in most cases allows only tenuous placement of Gulf reptant larvae into lower taxa. Most published larval descriptions of Gulf species are based on reared larvae of adults from populations outside the Gulf. For instance, the descriptions of the laboratory reared larvae of *Callinectes sapidus* (Costlow and Bookhout 1959) and *C. similis* (Bookout and Costlow 1977) from the United States east coast are inadequate for identification of their counterparts from the Gulf of Mexico (Andryszak 1979; Stuck, Wang and Perry 1981).

STUDY AREA, MATERIALS, AND METHODS

Zooplankton samples were collected on Cruise 67, July 6–16, 1976, of the RV *Oregon* II (NOAA, National Marine Fisheries Service). Cruise 67 was a trawl survey of the northern Gulf of Mexico industrial bottomfish grounds, and zooplankton sampling stations were selected from the groundfish cruise track. Thirty-three zooplankton stations (Fig. 1) in depths of 9–91 m were sampled east and west of the Mississippi River delta within an area bounded by meridians 88° 04′W and 91° 17′W.

All collections were made with a 61 cm bongo sampler (Posgay, Marak and Hennemath 1968) equipped with 0.505 mm and 0.333 mm nylon mesh nets; a flow meter was mounted in the mouth of each net. Double oblique tows were made concurrently with 10-min trawl hauls for groundfish, and hence at trawling speeds (> 150 cm/sec). A dead weight of 45 kg attached to the bongo sampler allowed a towing angle of approximately 30°; at all but the deepest stations the sampler usually came within several meters of the bottom. The only exceptions to this bongo sampling procedure occurred at stations 11, 12 and 13 where winch problems resulted in horizontal tows being taken at approximately 1 m below the surface. At each station sea surface temperatures were taken with a hand-held thermometer and surface salinities determined by refractometer.

All samples were initially preserved in the field with 3–5% buffered formalin. Samples taken in the 0.505 mm mesh net and from which all larval fishes had been removed were picked for larval reptants. Most samples were divided into ½, ¼ or ⅛ portions prior to analysis using a Folsom plankton splitter. Wet displacement volumes (Smith and Richardson 1977) of total zooplankton (excluding larval fishes) and reptant larvae alone were determined for each sample. Larval reptants were separated under dissection and compound microscopes and assigned to the lowest practicable taxon. In most cases specific identification was not possible; and the lowest practicable taxon was designated a larval "kind". A kind included zoeas and megalopas if both could be referred to the same developmental series. In a few cases, megalopas could be identified to species, zoeas only to genus. Larval abundances were expressed as numbers under 1 m^2 of surface (number/m^2) at all stations except 11, 12, 13 where horizontal tows were taken and abundances expressed as numbers per cubic meter (number/m^3).

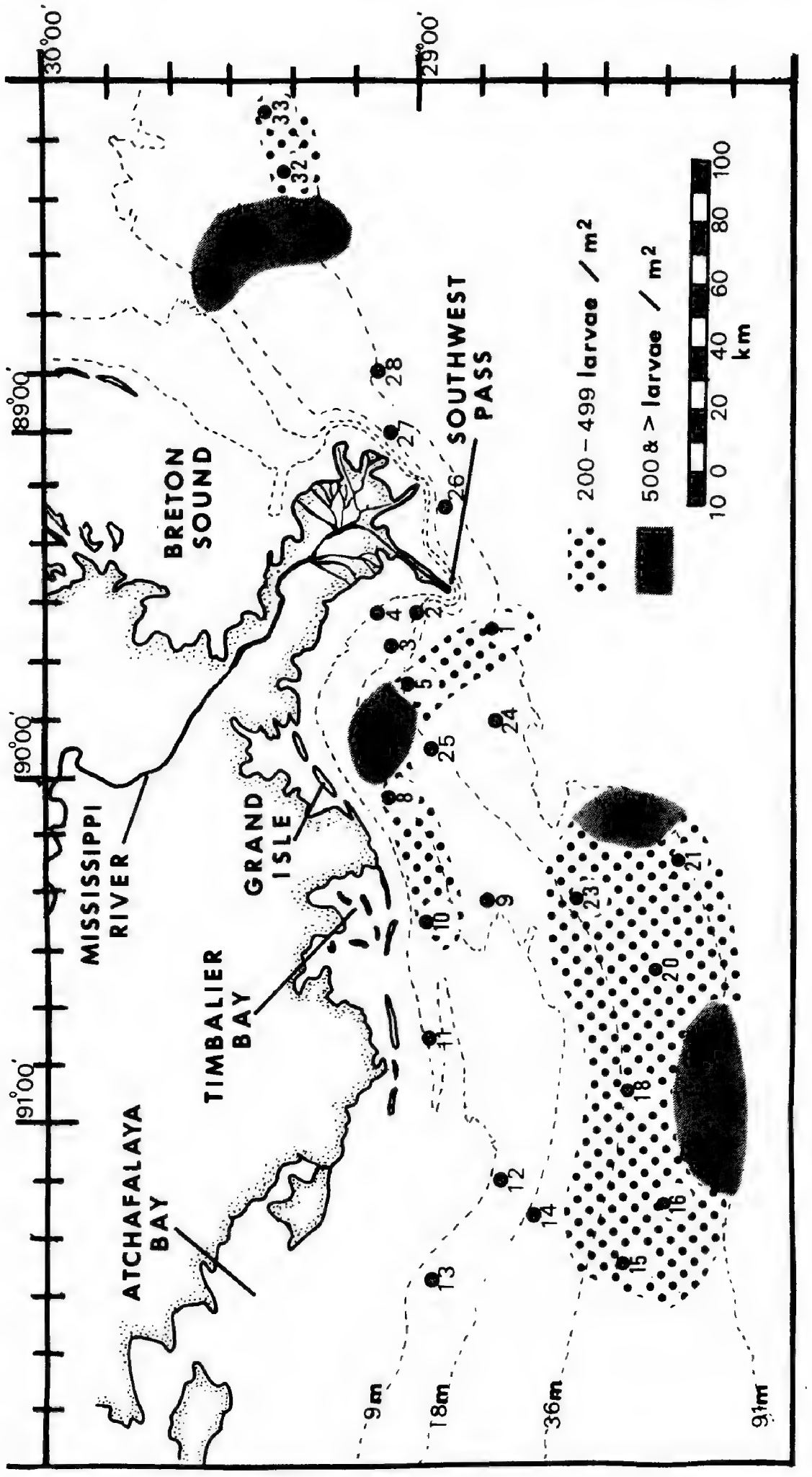

FIG. 1. Map of southeast Louisiana coast with sampling stations and areas of highest total larval reptant densities indicated.

RESULTS

WATER TEMPERATURE AND SALINITY

Surface water temperatures and salinities were typical of summer hydrography in the area (cf. Wiseman, Bane, Murray and Tubman 1975). Surface water temperatures were uniformly high (27.0–30.0°C) and surface salinities ranged from 18.0–34.0 ppt. Lowest surface salinities were associated with freshwater discharge from the major Mississippi River passes (e.g. 18, 20, 18 ppt at Stations 26, 27, 28, respectively) and with runoff from the Barataria Bay estuarine system (20 and 22 ppt at Stations 7 and 6, respectively). Highest salinities in the study area, 32–34 ppt, occurred at deepest stations west of the delta (Stations 16–22) beyond direct influence of Mississippi River discharge and basin runoff.

ZOOPLANKTON VOLUMES

Total zooplankton volumes were consistently high near shore west of the delta, and especially between Southwest Pass, Mississippi River delta and Grand Isle, Louisiana (Table 1). At each station, that part of the total zooplankton volume attributed to reptant larvae ranged from negligible to 27% (Table 1), but because of relatively small larval sizes the actual reptant volume was always low. Zooplankters whose numbers and bulk contributed most to high total displacement volumes were chaetognaths, sergestid shrimps (mostly *Acetes americanus* but also *Lucifer faxoni*); doliolids; small medusae and at a few stations, stomatopod larvae.

DISTRIBUTION AND ABUNDANCE OF LARVAE

General

Zoeas, and megalopas of 66 kinds of reptants representing at least 20 families were collected (Table 2). *Callinectes* spp. was most abundant, followed by *Uca* spp. and *Portunus* spp. Notes on identification and partial descriptions of many of the larvae mentioned here were presented in Andryszak (1979).

Total densities of reptant larvae varied greatly from station to station (Table 1), as did densities of each of the frequently occurring categories of larvae (Table 3). Greatest total densities of reptant larvae (Fig. 1) were usually associated with *Callinectes* spp. larvae. However, at Station 7 off Grand Isle where total larval reptant density was greatest (Table 1) *Uca* spp., *Panopeus* sp., *Neopanope texana* and *Callianassa major* reached their greatest individual abundances and *Callinectes* spp. made up only 40% of the total catch.

Anomura

Thalassinoid larvae were well represented in our samples. Representatives of both the "homarine" (Axiidae and Callianassidae) and "anomuran" (Upogebiidae and Laomediidae) groups of Gurney (1938) were collected (Table 2).

TABLE 1

Total zooplankton, reptant larval wet displacement volumes, and total reptant larval densities by stations, July 6–16, 1976. Stations 11,12,13(*) were horizontal tows and reptant densities are reported per m^3.

Station	Total Zooplankton ($cc/100m^3$)	Reptant ($cc/100m^3$)	Reptant Densities ($rept/m^2$)
1	52.0	4.7	265.1
2	58.1	6.1	99.1
3	44.6	2.3	55.7
4	11.2	0.6	89.1
5	83.0	3.8	234.9
6	31.2	3.8	1015.5
7	51.9	3.7	2069.2
8	58.2	3.8	221.6
9	29.6	2.4	192.2
10	ND	ND	414.0
11*	34.6	4.9	98.3
12*	58.7	Neg	15.9
13*	38.0	7.0	51.3
14	38.2	4.3	132.9
15	26.4	0.6	452.6
16	17.3	0.2	385.4
17	15.7	2.1	1244.9
18	5.3	1.4	272.9
19	25.1	4.0	703.8
20	13.3	0.9	476.4
21	6.1	0.5	482.9
22	11.5	1.4	917.2
23	15.5	0.7	220.2
24	17.8	1.8	167.1
25	57.4	Neg	75.9

TABLE 1 (continued)

26	21.6	1.7	129.6
27	43.9	2.1	67.8
28	41.2	0.9	183.9
29	42.3	4.9	879.7
30	20.8	4.0	597.0
31	21.5	3.0	655.9
32	40.4	5.1	320.7
33	41.1	0.4	251.4

ND-no volume determination
Neg-negligible volume of reptant larvae

The callianassid designated *Callianassa* sp.A was collected at 70% of the stations while most others were infrequently taken (Table 2). *Callianassa major* was present at only six stations (all shallower than 22 m) although abundance at one station (Station 7) was 47.6/m^2. Larvae of *Upogebia affinis* were infrequently taken; the highest concentration was 4.5/m^3 (Station 11). Laomediid sp. occurred frequently (Table 2) mainly at stations deeper than 27 m; highest concentrations (9.6–23.8/m^2) were found at stations 15, 17, 19, 25, and 26. Although larvae of laomediid sp. were frequently collected and moderately abundant at some stations we found only one reference (Ngoc-Ho 1981) to the occurrence of a similar form in previous North American plankton studies. Ngoc-Ho (1981) described larvae attributed to *Axianassa* of the Laomediidae collected in the Gulf of Mexico. Our larvae are very similar to those described by Ngoc-Ho (1981) and to a laomediid described by Gurney (1938), p. 337–338, Fig. 38) from the western South Atlantic off Brazil. We found no reference to the occurrence of any adult Laomediidae from the northern Gulf of Mexico but Gurney (1938) stated ". . . our present knowledge of the adults [Thalassiniodea] is quite inadequate to account for the types of larvae known. The larva is easily captured, the adult may not be and it is probable that many more adult species remain to be discovered . . .". When the present samples were studied only six species of thalassinoids were known from the northwestern Gulf of Mexico (Felder 1973), mostly estuarine and nearshore forms. Recently, Rabalais, Holt and Flint (1981) reported six more species from the northwestern Gulf.

Diogenid and pagurid hermit crab larvae were frequently taken and several are discussed in detail below. One galatheid larva was collected (Station 20) and small numbers of three species of porcellanids were infrequently encountered (Table 2). Only 10 specimens of a hippid, *Emerita*

TABLE 2

Reptant larvae and frequency of occurrence at 33 stations, July 6–16, 1976. Z = Zoeas; M = Megalopas.

Larvae	Developmental Stages	Frequency of Occurrence
Anomura		
Thalassinoidea		
thalassinoid sp. A	Z	1
axiid (?) sp. A**	Z	13
axiid (?) sp. B	M	2
laomediid sp.	Z	18
*Callianassa major**	Z	6
Callianassa sp. A	Z	23
Callianassa sp. B	Z	6
Callianassa spp.	M	5
Upogebia affinis	Z	9
Paguroidea		
Clibanarius vittatus	Z M	15
Paguristes (?) sp.	Z	2
diogenid (?) sp.	Z	2
*Pagurus pollicaris***	Z	10
Pagurus sp.*	Z M	11
pagurid sp. A	M	1
pagurid sp. B	M	1
Galatheoidea		
galatheid sp.	Z	1
*Porcellana sigsbeiana***	Z	4
*Polyonyx gibbesi**	Z	8
Euceramus praelongus	Z M	6
Hippoidea		
Albunea spp.	Z	32
Lepidopa spp.*	Z M	6
Emerita sp.*	Z	3
Brachyura		
Oxystomata		
Ethusa sp.**	Z	18
Calappa spp.**	Z M	19
leucosiid sp. A	Z	31
leucosiid sp. B	Z	1
Oxrhyncha		
Libinia spp.	Z	3
Libinia dubia	M	2
Libinia emarginata	M	1
Brachyrhyncha		
Arenaeus cribrareus	M	2
Callinectes spp.	Z	33
Callinectes sapidus	M	32
Callinectes similis	M	32
Portunus sayi (?)	Z	1
Portunus spp.	Z M	33
portunid sp	M	2
Hexapanopeus (?) sp.	M	1
Menippe sp.	Z M	15
Neopanope texana	Z M	29
Panopeus sp.	Z	18
Rhithropanopeus harrisii	Z	1
*Pinnixa chaetopterana**	Z	10
Pinnixa sp. A*	Z	8
Pinnixa sp. B*	M	6
Pinnixa (?) sp. C	Z	2
Pinnotheres maculatus	Z	4
pinnotherid (?) sp	Z	9
Sesarma cinereum	Z M	8
Ocypode quadrata	Z	1
Uca spp.	Z M	24
unidentified 18**	Z	11
unidentified 19	Z	3
unidentified 43	Z	1
unidentified 44	Z	1
unidentified 47	Z	1
unidentified 48	Z	1
unidentified 4	M	27
unidentified 11**	M	9

TABLE 2 (continued)

leucosiid (?) sp. C	M	19	unidentified 15	M	12
raninid sp. A	Z	2	unidentified 16**	M	4
raninid sp. B	Z	2	unidentified 27	M	2
			unidentified 33	M	1

* Nearshore, 70 - 100% of occurrences at stations < 36 m

** Offshore, 70 - 100% of occurrences at stations > 36 m

TABLE 3

Density ranges and means for frequently occurring reptant larvae (% occurrence > 0.50). Calculations based on densities among samples from 30 stations; Station 11, 12, 13 values not included.

Larvae	Density Range (larvae/m^2)	Density Mean ± SE	Coeff. Var.
Callianassa sp. A	0.00 - 12.16	2.17 ± 0.60	1.53
laomediid sp.	0.00 - 23.76	3.58 ± 1.06	1.63
Albunea spp.	0.00 - 84.24	23.13 ± 4.22	1.09
Ethusa sp.	0.00 - 15.12	1.84 ± 0.56	1.67
Calappa spp.	0.00 - 23.12	7.53 ± 1.11	0.81
leucosiid sp. A	0.00 - 53.82	8.08 ± 2.05	1.39
leucosiid sp. C	0.00 - 24.68	3.37 ± 1.19	1.94
Callinectes spp.	0.50 -1140.48	238.43 ± 56.80	1.30
Callinectes sapidus	0.00 - 58.96	11.68 ± 2.08	0.96
Callinectes similis	0.00 - 28.56	8.31 ± 1.23	0.80
Portunus spp.	0.88 - 249.00	37.00 ± 9.10	1.34
Neopanope texana	0.00 - 89.92	12.37 ± 3.66	1.62
Panopeus sp.	0.00 - 187.92	10.65 ± 6.30	3.23
Uca spp.	0.00 - 781.84	53.01 ± 26.29	2.71
unidentified 4	0.00 - 61.03	7.22 ± 2.34	1.77

sp., were collected. Larvae of *Lepidopa* spp. were infrequently taken (Table 2), but *Albunea* spp. larvae occurred at all but one station (Table 2). *Albunea* spp. was more abundant (densities > 24/m^2) at stations deeper than 21 m; maximum abundance (Table 3) occurred at Station 19 (64 m).

Brachyura

Larvae of the four families of oxystomatous crabs were represented in our samples. Two larvae each of raninid sp.A and raninid sp.B were taken at stations deeper than 34 m. Larvae of the dorippid, *(Ethusa* sp.), and calappids *(Calappa* spp.) were widely distributed offshore (mostly stations > 36 m) in almost an identical manner. At least two species of *Calappa* larvae were present; one advanced zoea had well developed cheliped buds which resembled chelipeds of *Calappa flammea* megalopas (Lebour 1944). Leucosiid sp.A was taken at all but two stations; leucosiid (?) sp.C also occurred widely but was conspicuously absent from the deepest stations in the western part of the study area (Stations 16–23).

Only a very few oxyrhynchous larvae were collected and these were of *Libinia* (Majidae). Three specimens were zoeas and four were megalopas; the latter could be identified to species (Johns and Lang 1977) but the former could not.

Portunids, the most abundant larvae collected are discussed below. Xanthid larvae were numerous. *Neopanope texana* was fifth in abundance (Table 3); its larvae, especially the zoeas, were most abundant at stations shallower than 24 m. Zoeas of *Panopeus* sp. occurred (Table 2) over the entire study area but were most abundant nearshore off Grand Isle (Stations 6–7). No megalopas of *Panopeus* sp. were collected. Small numbers of zoeas and megalopas of *Menippe* sp. were taken at stations scattered over all but the deepest stations in the western portion of the study area (Stations 15–22). Although similar to stone crab larvae described by Porter (1960) and Scotto (1979), comparison with laboratory reared specimens (Truesdale unpublished) has confirmed that these larvae are of an undescribed *Menippe* of the Gulf of Mexico (D. L. Felder personal communication). One zoea of the estuarine xanthid *Rhithropanopeus harrisii* was taken at Station 27. This crab undergoes its larval development in low salinity areas (Chamberlain 1962) and recruitment to adult populations is through retention in estuaries (Sandifer 1975). Our specimen was probably swept from nearby low salinity delta marshes.

More kinds of pinnotherid larvae were collected than those of any other brachyuran family (Table 2). *Pinnixa chaetopterana* larvae were predominant and greatest numbers occurred at stations shallower than 18 m; they were absent from deep water western stations (Stations 15–23). *Pinnixa* sp.A similar to *P. sayana* larvae of Hyman (1925), occurred mainly at stations shallower than 18m. Small numbers of *Pinnotheres maculatus* larvae were also collected.

Adults of *Uca* spp., *Ocypode quadrata* (Oxypodidae) and *Sesarma cinereum* (Grapsidae) are semi-terrestrial. Larvae swept offshore must regain a suitable beach if they are to be recruited to the adult populations. The

distribution of *Uca* spp. is discussed below. *Ocypode quadrata* is abundant on sandy Gulf beaches of the study area (Felder 1973) but only one larva (zoea I) was collected (Station 26). Sandifer (1973) found no *O. quadrata* larvae during his study of Chesapeake Bay although he remarked that adult populations were abundant in the lower bay. Goy (1976), who also worked in Chesapeake Bay, collected only three larval specimens of *O. quadrata* (zoea I, II, V). Crane (1940) reported that *Ocypode* megalopas have been collected in the surf zone and on ocean beaches where molting to first crab occurs.

Sesarma cinereum was not abundant and occurred infrequently (Table 2) but all developmental stages except zoea I were represented. Several larvae (zoea II–IV) were collected east of the delta (Stations 30–33); all other occurrences were in close proximity to shore. Highest abundance was 8.7/m^2 (Station 7). Shipp (1977) collected large numbers of *S. cinereum* larvae in a saltmarsh area of Mobile Bay, Alabama; all her larvae were zoea I except for two zoea II and one megalopa.

MOST ABUNDANT KINDS

Although four species of *Callinectes* have been reported for our study area (Felder 1973; Perry 1973), *C. sapidus* and *C. similis* are by far the most common. We believe our *Callinectes* spp. (zoeas) were predominately of these two species. Zoeas and megalopas of *C. sapidus* and *C. similis* are very similar in morphology and existing literature on the larval development of these two species from east coast stocks (Bookout and Costlow 1977) would not allow their reliable separation from Gulf plankton material. Recently Stuck *et al.* (1981) and Stuck (personal communication) reported characters that allow separation of Gulf *C. sapidus* and *C. similis* megalopas. Among our megalopas originally roughly sorted as *Callinectes* spp., were two megalopas of *Arenaeus cribrarius* from Stations 29 and 30 and two megalopas of an unknown portunid from Stations 15 and 17. The ratio of total *C. sapidus* megalopas to *C. similis* was 1.2:1, and mean abundances were not greatly different (Table 3). Megalopas of *C. sapidus* and *C. similis* occurred together at all but one station; no *C. sapidus* megalopas were taken at Station 17 and no *C. similis* at Station 23. Distribution and relative abundances of *C. sapidus* and *C. similis* megalopas showed no distinct patterns in the study area (Fig. 2A); at many stations both were found in almost equal numbers.

Early zoeas (zoea I, II) and megalopas *(C. sapidus* and *C. similis* combined) comprised the greatest percentage of total *Callinectes* larvae at nearshore stations, and intermediate and advanced stage zoeas occurred most frequently at offshore stations (Fig. 2A). These findings are similar to those reported for *Callinectes* spp. larvae on the east coast of the United States (Nichols and Keney 1963; Tagatz 1968; Dudley and Judy 1971) and support what Smyth (1980) calls "the developmental model of *Callinectes, i.e.,* larval development in shelf waters and subsequent recruitment to inshore and estuarine adult populations. . . ."

Four species of *Portunus* occur in the study area but *P. gibbesii* and *P. spinicarpus* are most abundant and are ovigerous throughout the year

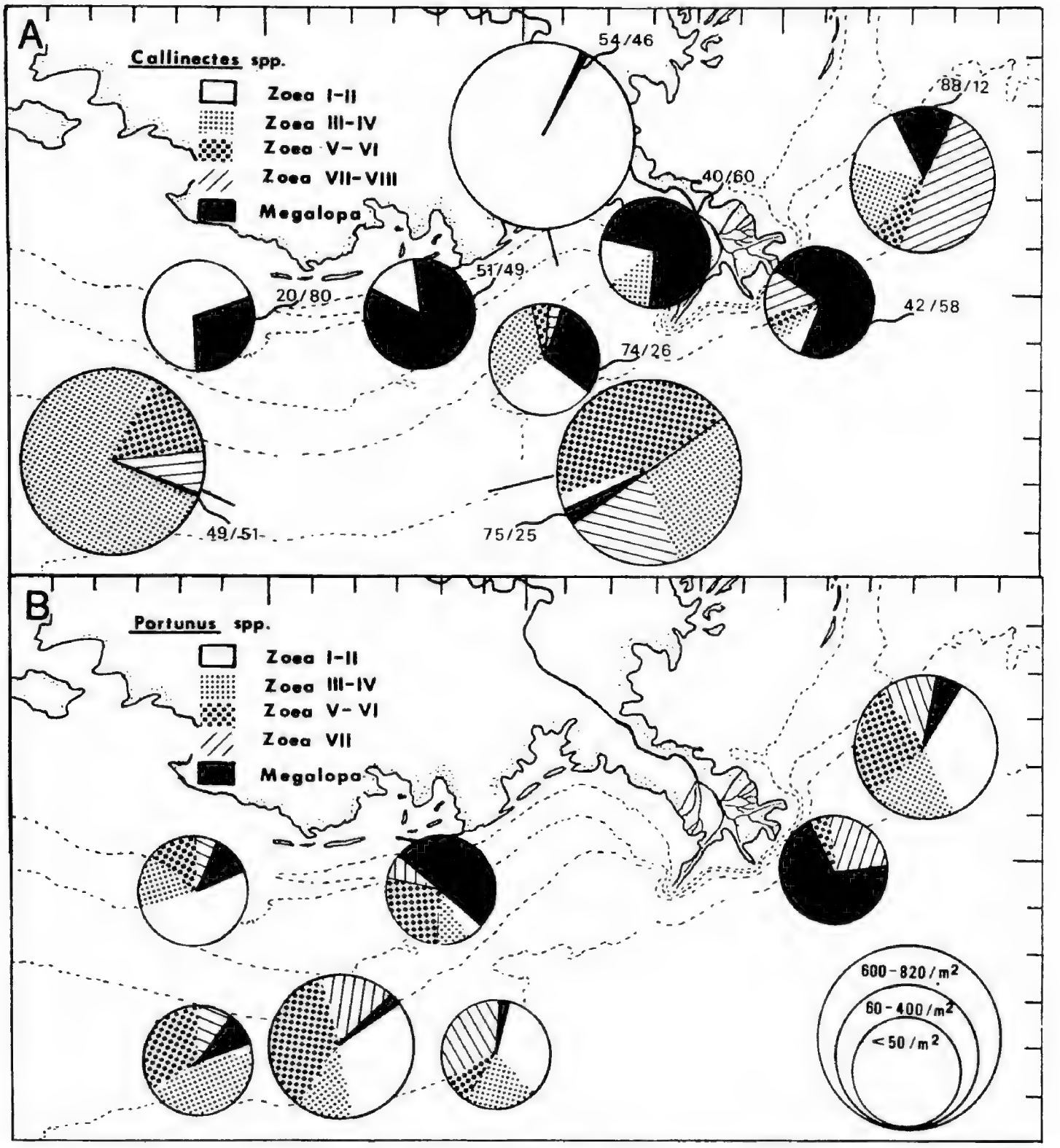

FIG. 2. Distribution of portunid larval stages. (A) Percent composition of *Callinectes* spp. larval stages for 18 stations. Values associated with each diagram are percent *C. sapidus* megalopas to *C. similis* megalopas. (B) Percent composition of *Portunus* spp. larval stages for 14 stations. Each diagram represents average density and percent composition of stages for two consecutive stations.

(personal observations). We believe our *Portunus* spp. larvae were mostly *P. gibbesii* and *P. spinicarpus*. Distributional patterns of the various developmental stages of *Portunus* spp. were not distinct (Fig. 2B). Although *Portunus* spp. occurred at all stations, their densities were relatively low in the bight immediately west of the delta and in western offshore areas, where *Callinectes* densities were very high.

Five species of the semiterrestrial fiddler crabs, *Uca,* occur in the study area. *Uca* larvae are morphologically very similar and cannot be separated to species at this time. *Uca* spp. have 5 zoeas and a megalopa (Hyman 1920); zoea III–V and megalopa were most common in our samples. Zoea II was comparatively rare, found only at 4 stations (Stations 6, 5, 8, 11) all shallower than 22 m. No zoea I was collected; this is probably due to the completion of this stage near shore where no samples were taken. West of the delta, greatest concentrations of *Uca* spp. were found at nearshore stations in the coastal bight (Louisiana Bight) between Southwest Pass and Timbalier Bay (Fig. 3A). *Uca* spp. larvae were absent from the offshore western part of our study area (Fig. 3A).

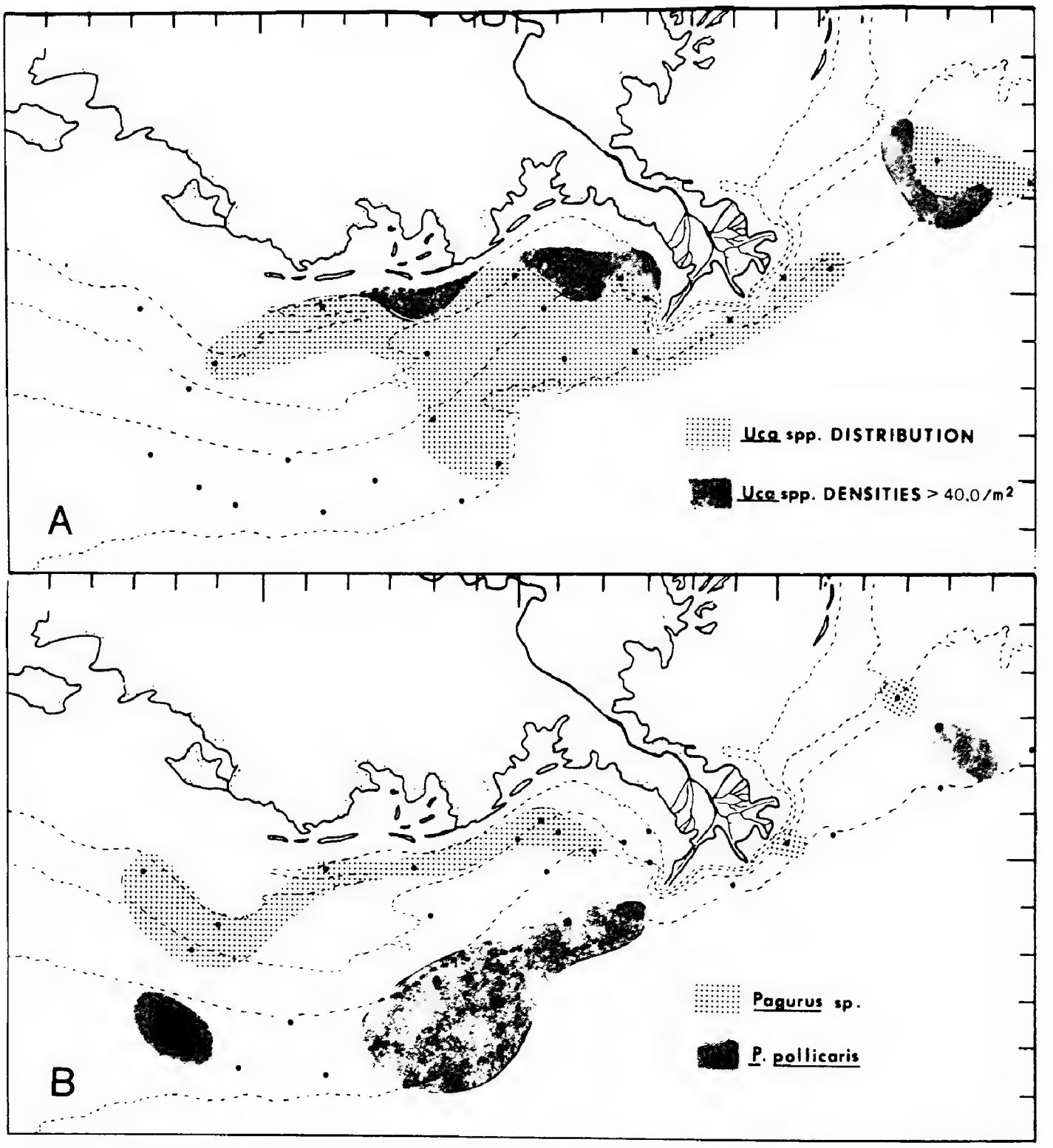

FIG. 3. Selected larval distribution patterns. (A) Distribution of second most abundant kind, *Uca* spp., (B) Nearshore and offshore distribution, respectively, of *Pagurus* sp. and P. pollicaris larvae.

DISCUSSION

NEARSHORE AND OFFSHORE DISTRIBUTION

Larvae of eight kinds of anomurans and pinnotherid brachyurans were collected mostly at nearshore stations (Table 2). Adults of most of these larvae are primarily nearshore marine and estuarine inhabitants (Felder 1973).

Larvae collected exclusively at offshore stations (Table 2) *e.g. Porcellana sigsbeiana, Ethusa* sp. and *Calappa* spp. are of species whose adults occur in sub-littoral and deeper offshore waters (Felder 1973, Powers 1977). Many rarely occurring larvae, including the greatest number of unidentifiable larvae were collected at offshore stations. We believe many of these rare larvae are representatives of taxa, which are non-neritic as adults, and their presence in the outer study area suggests intrusion of oceanic waters.

Pagurus sp., similar to *P. annulipes* of Nyblade (1970), and *P. pollicaris* respectively offer clear examples of nearshore and offshore distributions (Fig. 3B). We collected all four zoeal stages and the megalopa of *Pagurus* sp. Zoea III–IV occurred most frequently, zoea II and megalopa occasionally, but zoea I occurred at only 1 station. We collected all 4 zoeal stages of *P. pollicaris* but no megalopas; zoea II and IV were most abundant. Fotheringham and Bagnall (1976) reported larvae of *Pagurus annulipes* and *P. pollicaris* from Christmas Bay near Galveston Texas. *Pagurus annulipes* does not occur in the Gulf of Mexico (Lemaitre, McLaughlin and Garcia-Gomez 1982), but as the source of identification of the larvae was Nyblade (1970), we assume Fotheringham and Bagnall's (1976) *P. annulipes* is the same as our *Pagurus* sp. Fotheringham and Bagnall (1976) found many larvae (all stages) of *"P. annulipes"* in their collections but collected only 4 *P. pollicaris,* all zoea I. These findings are consistent with our categorizing *Pagurus* sp. as dwelling nearshore, *P. pollicaris* offshore.

Fotheringham and Bagnall (1976) collected large numbers of *Clibanarius vittatus* zoea I and the megalopa from Christmas Bay Texas, but no zoea II–V; they also noted large numbers of very small juveniles. We collected all but zoea IV of *C. vittatus;* all zoea I were collected nearshore (<22 m) and zoea III and V were collected at offshore stations (Stations 21, 22, 24). Megalopas were scattered among offshore and nearshore stations. Our findings and those of Fotheringham and Bagnall (1976) suggest that *C. vittatus* may spawn within estuarine water bodies but development occurs offshore and recruitment back onshore and into the estuary is by megalopas and early crab stages.

LARVAL DISTRIBUTION AND HYDROGRAPHY

The distribution and abundance of reptant larvae reflect not only circulation patterns but also the biology of particular species, *e.g.* spawning areas, length of pelagic larval life and larval behavior, particularly vertical movement (Sandifer 1973; Sulkin, Van Heukelem, Kelley and Van Heukelem 1980). Recent hydrographic studies (Wiseman *et al.* 1975; Wiseman, Murray,

Tubman and Bane 1976) have provided surface circulation patterns and vertical structure for a part of our study area, the Louisiana Bight. Our oblique bongo tows however, yielded no vertical distributional data on larvae and hence no elucidation of larval transport mechanisms was possible.

Three areas of very high larval reptant abundance were indicated by our samples, two offshore, east and west of the Mississippi delta and one nearshore off Grand Isle, Louisiana (Fig. 1). In the latter area, particularly at Station 7 where the highest larval reptant density of the study was recorded, most of the abundant larvae were of reptants thought to spawn in the immediate area or on nearby shores. Early and late developmental stages of most of these reptants other than *Callinectes* spp. at Station 7, indicated that complete larval development occurs nearshore. Horizontal distribution of larvae probably paralleled closely the adult distributions as Sandifer (1975) found for a number of estuarine crabs in Chesapeake Bay.

High larval abundances in the two offshore areas (Fig. 1) consisted almost exclusively of portunids (Fig. 2A-B). The east offshore area was very high in both numbers of *Callinectes* spp. and *Portunus* spp.; the west offshore was predominately *Callinectes* spp. If large numbers of *Callinectes* spp. zoeas were *C. sapidus,* transport mechanisms must be operative in the study area to effect both their offshore concentration and also the transport back onshore of *C. sapidus* megalopas. Sulkin *et al.* (1980) reported that as development progresses *C. sapidus* larvae tend to concentrate in deeper layers of the water column. This suggests that offshore concentrations may be effected by surface currents and recruitment (shoreward) by bottom currents. Wiseman *et al.* (1975) and Wiseman *et al.* (1976) have demonstrated strong vertical stratification in the Louisiana Bight during all months. Currents above the halocline were variable in time and space due to tidal effects, wind direction and speed, and Mississippi River discharge; bottom currents were onshore for a large portion of the year (Wiseman *et al.* 1975; Wiseman *et al.* 1976).

We have demonstrated that a large concentration of advanced *Callinectes* spp. larvae occur in offshore waters of Louisiana along with advanced larvae of a few other nearshore reptants (e.g. *Clibanarius vittatus* and *Pagurus pollicaris).* However, elucidation of dispersal and recruitment mechanisms awaits intense zooplankton sampling at discrete depths with concurrent hydrographic monitoring.

ACKNOWLEDGMENTS

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BEHAVIORAL ASPECTS OF JUVENILE PENAEID SHRIMPS, *P. AZTECUS* AND *P. DUORARUM*, DURING TIDAL TRANSPORT

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ABSTRACT

Behavioral patterns displayed by juvenile brown *(Penaeus aztecus)* and pink *(P. duorarum)* shrimp during descent through a water column were determined in the laboratory by observing individual shrimp placed in a clear plexiglass tube containing brackish water one meter deep. Behavior displayed during descent was used to create ethograms (behavioral maps) for each species. Rates of vertical descent were determined for shrimp treated by cold shock and for shrimp that received no treatment. Effects of body shape and density were determined by observing sinking rates of freshly killed shrimp. Results indicated that juvenile brown and pink shrimp displayed a simple and predictable method of removing themselves from a water column in the laboratory, a method possibly similar to that used during tidal transport. Velocity of descent through the water column was controlled behaviorally by body posture, pleopod and leg activity, and approach to the substrate. Differences in rate of descent (9.5 to 27 cm s^{-1}) were attributable to the position of the walking legs—either retracted or extended—during descent and use of pleopods for propulsion. Descent rates are slow relative to estuarine tidal currents; therefore, shrimp may be transported laterally for several hundred meters while they are settling to the bottom. The ability to exit from the water column may be an important aspect of penaeid shrimp ecology if estuarine sediments preferred by shrimp are patchy in abundance.

INTRODUCTION

Water movement due to tides is widely recognized as an important transport mechanism for penaeid shrimp species. Postlarval penaeid shrimp utilize flood tides to immigrate to estuarine nursery areas from the ocean spawning grounds (Tabb, Dubrow and Jones 1962; Copeland and Truitt 1966; Hughes 1966; Duronslet, Lyon and Marullo 1972). Emigration of juvenile shrimp from estuaries to the ocean is associated with ebbing tides (Copeland 1965, King 1971, Laney 1981). Evidently, physical or chemical

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changes associated with tide reversal elicit a corresponding behavioral change that allows shrimp to utilize favorable tides for transport and to avoid displacement by unfavorable tides (Joyce 1965; Hughes 1969, 1972). The use of tides for transport allows migrations over great distances with a minimum amount of energy expended (C. B. Subrahmanyam, Florida A&M University, personal communication).

The behavior of penaeid shrimp swimming in the water column during tidal transport has not been studied extensively. Postlarval and juvenile brown shrimp, *P. aztecus,* exhibit diurnal vertical migration (King 1971, Duronslet *et al.* 1972). The effects of salinity changes on rheotactic behavior of juvenile pink shrimp, *P. duorarum,* were described from laboratory experiments by Hughes (1969). Juvenile pink shrimp were observed to swim above the bottom in a static water column for 12 hours or more (Aldrich 1963). Omori (1974) compared the maximum sinking velocities attained by populations of *Sergia lucens,* a pelagic Pacific shrimp, to the sinking rates of freshly killed specimens tested in the laboratory and determined that sinking rate was controlled voluntarily.

The objective of this study was to examine the method by which juvenile penaeid shrimp exit from the water column during tidal transport. This study also provides new information concerning behavior and rates of swimming that may be of use in understanding the ability of penaeid shrimp to remain in, or exit from, the water column during tidal transport. Maximum exiting responses by shrimp were elicited by conducting tests in a static water column under conditions of artificial lighting. Factors cuing penaeid shrimp to initiate vertical descent through a water column during tidal transport were not examined.

METHODS

From June through September, 1978, juvenile brown and pink shrimp were collected by trawl from the lower Cape Fear River estuary near Southport, North Carolina. Sizes ranged from 48 to 129 mm TL (tip of rostrum to tip of telson) for brown shrimp and 73 to 118 mm TL for pink shrimp. Test animals were held in floating cages and transferred to the laboratory just prior to testing. All tests were performed during daylight under conditions of artificial lighting and with ambient water temperatures (24.3 to 29.7 C) and salinities (12 to 24 ‰).

The test apparatus consisted of a vertical, transparent plexiglass tube 20 cm I.D. filled with brackish water to a depth of one meter. Concentric rings spaced at 10-cm intervals provided a visual scale for measuring shrimp movements. Light entering the tube was mostly restricted to the water surface by covering the side and bottom of the tube with black plastic; a vertical slit 7 cm wide was used to observe the behavior of each shrimp as it descended through the water column. An all-occurrences log (Altmann 1974) was used to record shrimp behavior. Time of day, salinity, and water temperature were recorded prior to each test.

A shrimp tested in a "normal" (no treatment) state was removed by net from the holding tank 15 min before the experiment and placed in a small bucket that contained just enough water to cover the body. This procedure curtailed swimming activity and restricted movement to crawling on walking legs. To start the test, the shrimp was removed from the bucket by the last abdominal segment and held over the water column in a head-down position. Pleopod activity began as the shrimp was submerged past the walking legs. Descent through the water column began upon release of the tail. The rate of descent was determined by dividing the distance of vertical descent by the time required to cover that distance. Data for a variety of states of

restfulness were generated by recapturing each shrimp and repeating the procedure until the animal could no longer maintain control of its body posture during descent. This method enabled a range of observations on behaviors displayed and on corresponding changes in rates of descent.

To determine whether sinking rates are involuntarily controlled, shrimp were subjected to sudden temperature drops. A shrimp was removed from water of ambient temperature and placed in water of 5 C for approximately 45 s. This cold shock treatment caused shrimp to lose swimming ability and control of body posture during descent. The sinking rate was determined by dividing the sinking distance by the time required to sink that distance.

To determine the effects of body shape and density on sinking rates, each shrimp tested as "normal" or as "cold shocked" was then sacrificed in undiluted (95%) ethanol at −5 C until all movement ceased (15 to 30 s). This caused the body to straighten with a slight bend at the third abdominal segment. The body was then submerged just below the surface of the water in a horizontal position with the ventral side up to allow the escape of air bubbles trapped within the pleopods. Sinking rate was determined in the same manner as for shrimp treated with cold shock. Total length (TL), carapace width (CW), carapace depth (CD), and wet weight were recorded for each shrimp after testing.

Preliminary studies indicated that behavior during descent was influenced by distance from the bottom. Therefore, behavior was studied under five criteria: (1) initial response at the surface after release, (2) body posture during descent, (3) pleopod and leg activity, (4) approach to the substrate, and (5) after-test activity. These criteria were then coded numerically for statistical analysis.

Differences in rates of descent due to body dimensions and the displays of various behaviors were analyzed by linear regression using the General Linear Models (GLM) procedure (SAS Institute 1979). Significant differences in descent rates as a function of the various behaviors displayed were determined by Duncan's multiple range test. Differences in behavior displayed by brown and pink shrimp were tested for significance by a two-sample Z-test for proportions (Remington and Schork 1970, p. 218).

RESULTS

Penaeus aztecus

The rate of descent through the water column was controlled by behavior and had no apparent relationship with body size. The average descent rate of brown shrimp with no treatment was significantly related to behavior displayed during descent ($P<0.01$, $r^2=0.49$, $df=138$) but was not related ($P>0.05$) to any dimensions of the body (TL, CW, and CD). These significant changes in descent rates were attributable to position of the walking legs during descent and to use of pleopods for propulsion. All brown shrimp that extended walking legs throughout descent, or that initially kept legs retracted and then extended them as they approached the bottom, exhibited significantly lower descent rates than those shrimp that kept legs retracted throughout descent (Table 1). Shrimp that drifted during descent (9%) did not use pleopods for propulsion and had slower descent rates than those shrimp that swam during descent.

A well-defined behavioral pattern was displayed by brown shrimp during descent through the water column (Fig. 1). Upon release at the surface, a majority (67%) of brown shrimp swam vigorously to the bottom in a nearly vertical, head-down posture. Pleopods were used for propulsion and the walking legs were retracted. The majority of brown shrimp swam to the

TABLE 1

Descent rates of juvenile brown shrimp *(P. aztecus)* that display various behavioral patterns in a water column. Significant differences were determined by Duncan's multiple range test. Descent rates, with their corresponding responses, connected by vertical lines are not significantly different ($P>0.05$).

Statistical grouping	Initial response	Position of walking legs	Approach to substrate	N	Mean descent rate ($cm\ s^{-1}$)	SD
I	Swim vigorously to bottom	Retracted	Swim into bottom head-first	73	26.5	0.79
I	Swim horizontally or tail kick, then proceed to bottom	Retracted	Swim into bottom head-first	20	27.3	1.49
II	Swim horizontally or tail kick, then proceed to bottom	Retracted	Stop or slow down near bottom by extending legs	6	19.1	2.71
II	Drift, vertical head down	Retracted	Drift	1	19.4	
III	Swim in circles to bottom	Retracted	Stop or slow down near bottom by extending legs	15	16.1	1.71
III	Swim vigorously to bottom	Retracted	Stop or slow down near bottom by extending legs	17	13.9	1.61
III	Swim vigorously to bottom	Extended	Drift	1	13.5	
III	Drift, horizontal upright	Extended	Drift	4	8.8	3.32
III	Drift, vertical head-down	Extended	Drift	2	7.4	

bottom head-first with no indication of sensing the approaching substrate by slowing the rate of descent. Each settled in a horizontal, upright position on the bottom and remained there until captured by net. The average rate of descent for this behavior was 26.48 cm s^{-1} (Table 1).

Approximately 17% of brown shrimp tested responded initially to release by swimming horizontally at the surface or by displaying a tail kick (closure of anterior and posterior portions of the body with a quick snap), and then proceeded to the bottom with walking legs retracted. The average descent

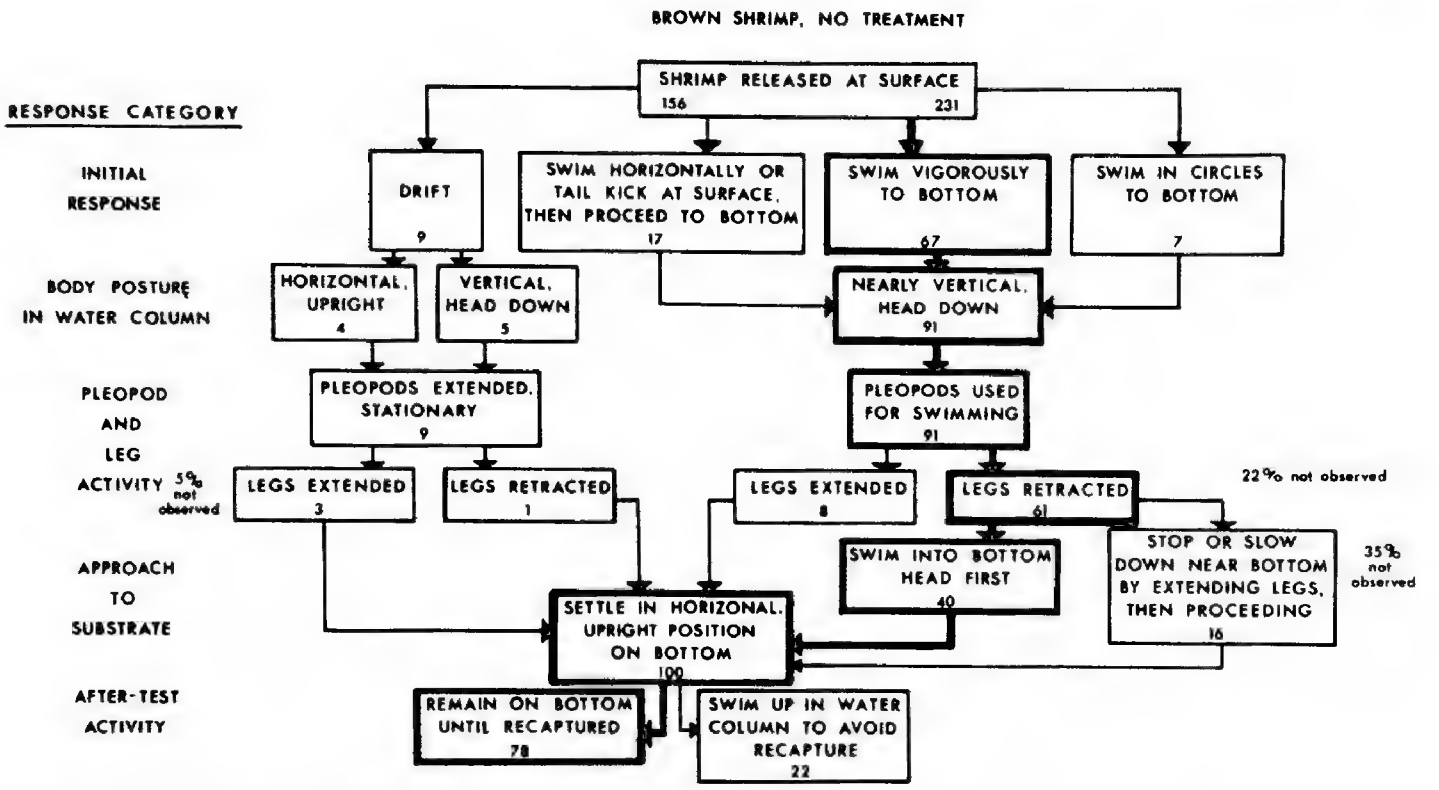

FIG. 1. Ethogram of the behavioral patterns of untreated juvenile brown shrimp, *P. aztecus*, during descent through a water column. Numbers are percent observed for each response (N=231 partial, 156 complete observations). Heavy boxes indicate the most common responses displayed.

rate for this response was 27.29 cm s^{-1}, which was not significantly different ($P>0.05$) from the rate for those individuals that descended immediately (Table 1).

Brown shrimp tested by cold shock and those tested as freshly killed did not have similar body positions during descent (Fig. 2). Response of the animals to cold shock was to curl the body; only 9% kept the body straight during testing. The majority (95%) of the freshly killed shrimp remained straight during the tests. The sinking rates of the two treatments were not significantly different ($P>0.05$, Duncan's multiple range test).

The larger, freshly killed brown shrimp sank more quickly through the water column than did the smaller shrimp tested in a similar fashion (Fig. 3). Sinking rates of freshly killed brown shrimp were positively related to total length ($P<0.01$, $r^2=0.50$, $df=44$). Also, the depth and width of the carapace (CD, CW) were significantly correlated with sinking rate ($P<0.01$, $r^2=0.50$, $df=44$).

Penaeus duorarum

The range of behaviors displayed by pink shrimp during testing was not as extensive as for brown shrimp. This may have been due to a smaller sample size (5 individuals for a total of 30 tests), which also precluded valid statistical comparisons for portions of the data. In the majority of tests (53%, or 16), pink shrimp swam vigorously to the bottom in a nearly vertical, head-down position by use of pleopods for propulsion while extending walking legs. Each settled in a horizontal, upright position on the bottom and

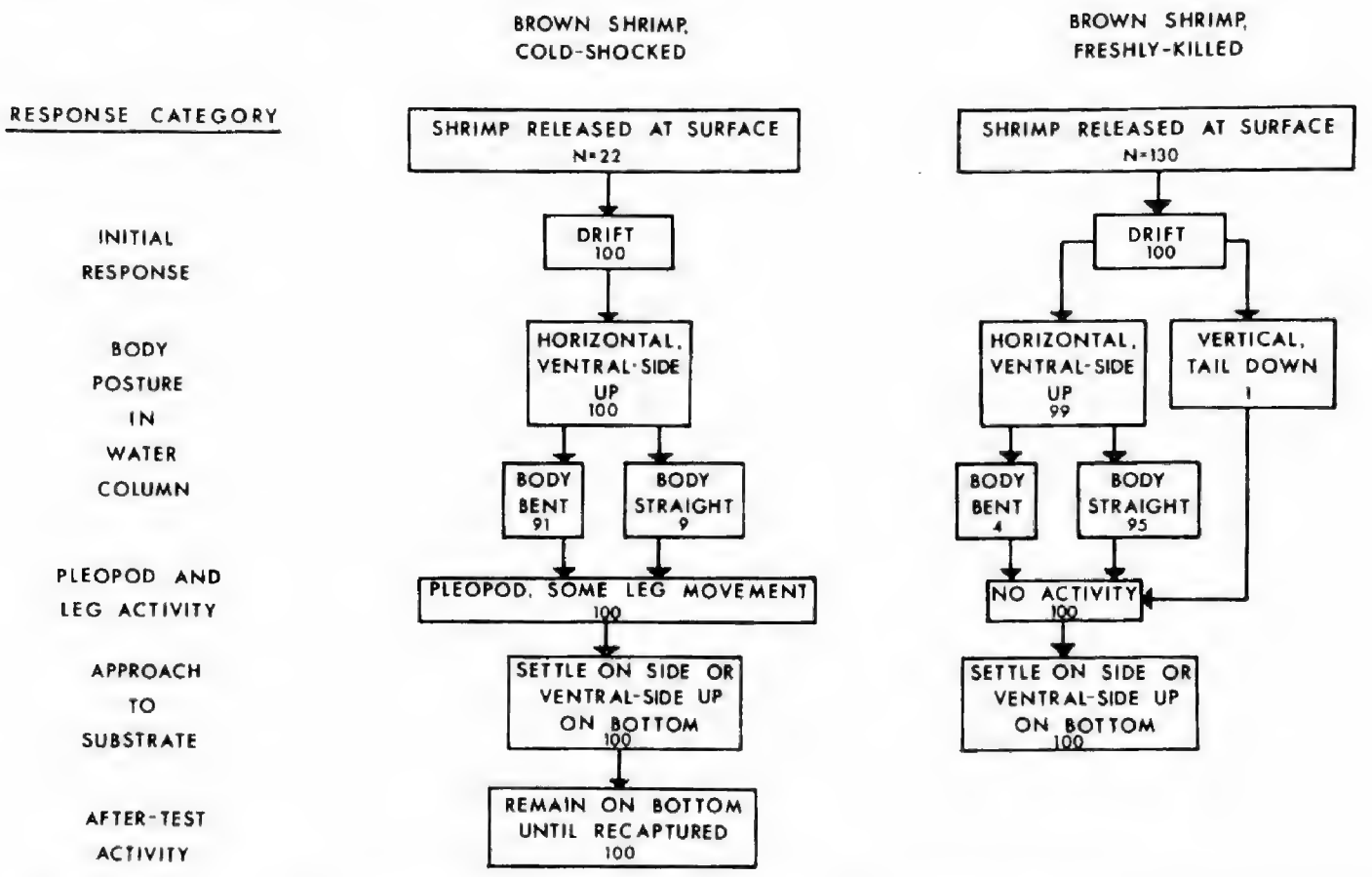

FIG. 2. Ethograms of cold shocked or freshly killed juvenile brown shrimp. Numbers are percent observed for each response.

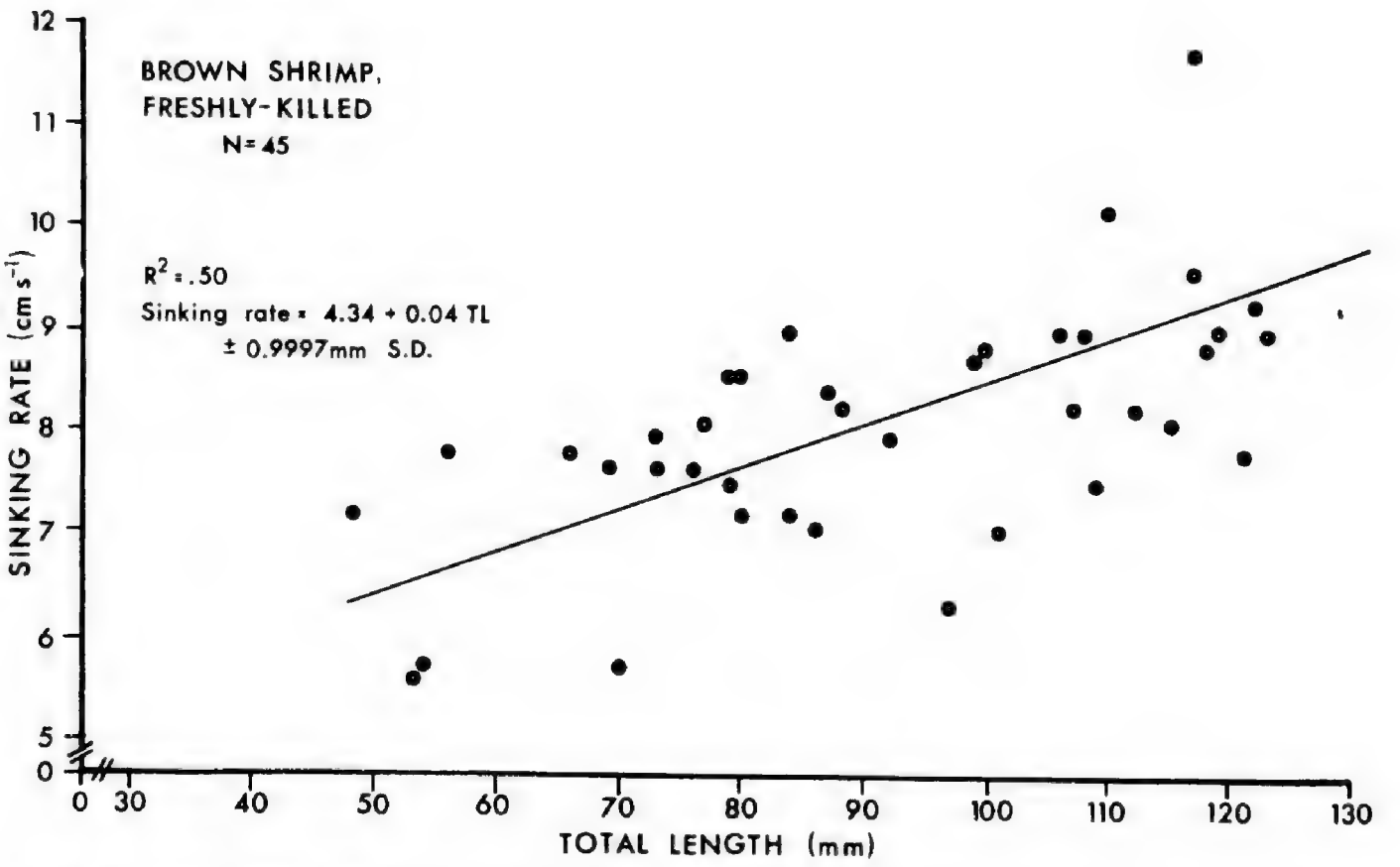

FIG. 3. The effect of total length on the sinking rate of freshly killed brown shrimp.

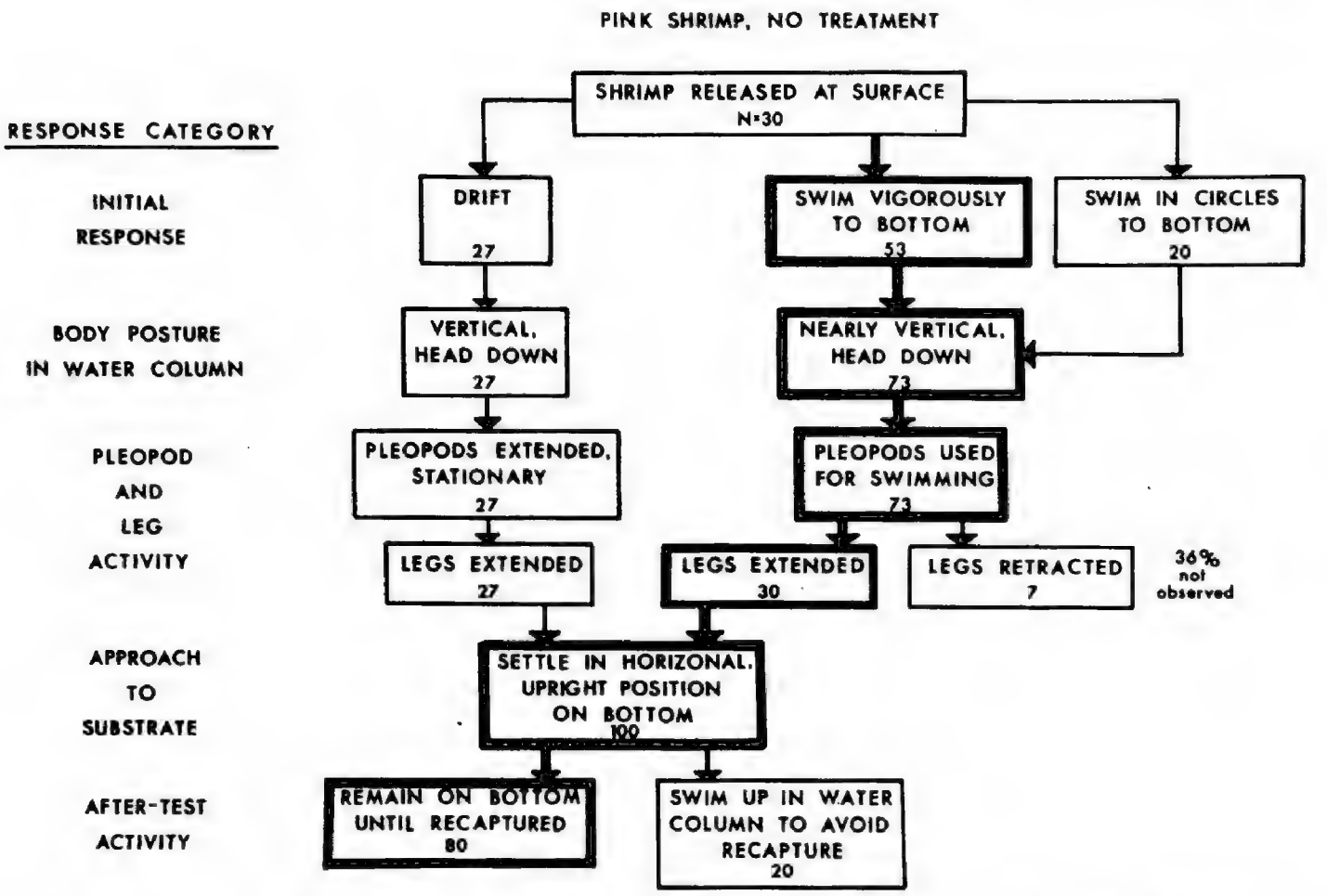
PINK SHRIMP, NO TREATMENT
RESPONSE CATEGORY
INITIAL RESPONSE
BODY POSTURE IN WATER COLUMN
PLEOPOD AND LEG ACTIVITY
APPROACH TO SUBSTRATE
AFTER-TEST ACTIVITY
SHRIMP RELEASED AT SURFACE N=30
DRIFT 27
SWIM VIGOROUSLY TO BOTTOM 53
SWIM IN CIRCLES TO BOTTOM 20
VERTICAL, HEAD DOWN 27
NEARLY VERTICAL, HEAD DOWN 73
PLEOPODS EXTENDED, STATIONARY 27
PLEOPODS USED FOR SWIMMING 73
LEGS EXTENDED 27
LEGS EXTENDED 30
LEGS RETRACTED 7
36% not observed
SETTLE IN HORIZONAL, UPRIGHT POSITION ON BOTTOM 100
REMAIN ON BOTTOM UNTIL RECAPTURED 80
SWIM UP IN WATER COLUMN TO AVOID RECAPTURE 20

FIG. 4. Ethogram of the behavioral patterns of untreated juvenile pink shrimp, *P. duorarum*, during descent through a water column. Numbers are percent observed for each response. Heavy boxes indicate the most common responses displayed.

remained there until captured (Fig. 4). In only 2 tests did pink shrimp descend with walking legs retracted, although this behavior was common to most brown shrimp. Descent by drifting, with pleopods extended and stationary, occurred more frequently ($Z = 2.16$, $P = 0.03$) in tests of pink shrimp (27%) than in tests of brown shrimp (9%). The average rates of descent for all pink shrimp behaviors displayed were not significantly different ($P>0.05$, Duncan's multiple range test), perhaps due to sample size. The average descent rate was 9.51 cm s^{-1}, similar to that for brown shrimp that descended through the water column by drifting with legs extended (Table 1). Freshly killed pink shrimp assumed the same body postures as brown shrimp that were cold shocked (Fig. 4). The effect of cold shock on pink shrimp was not tested.

DISCUSSION

Data indicate that penaeid shrimp must actively expend energy to remain in the water column during tidal transport and to exit voluntarily from the water column. Data from the three treatments—normal, cold shocked, and freshly killed—suggest that no involuntary mechanism is used to slow or inhibit descent. Omori (1974) reached the same conclusion after examining the sinking rates of *Sergia lucens,* a pelagic Pacific shrimp.

The causative factors that elicit exit from the water column remain unclear. Possible factors may be predator avoidance, substrate selection, swiftness of estuarine currents relative to the substrate, or changes in salinity (Rulifson 1980, 1981). Penaeid shrimp are capable swimmers; postlarval brown shrimp can swim above the substrate for 12 hours or more in the laboratory (Aldrich 1963) and can attain swimming speeds of 4.76 cm s^{-1} (Aldrich 1966). Juvenile brown shrimp 39 to 58 mm TL are capable of maintaining position in a 21 cm s^{-1} current (salinity 12 to 22 ‰, temperature 22.8 to 26.5 C) for several minutes by use of pleopods for propulsion (Rulifson, unpublished data). Pink shrimp can maintain position relative to the bottom against currents in excess of 26 cm s^{-1} (Fuss and Ogren 1966). None of these experiments examined the effects of salinity changes on swimming shrimp.

A study by Hughes (1969) demonstrated that juvenile pink shrimp normally orient and swim against a current in the laboratory, but decreased salinity elicited rheotactic reversal, which caused the animal to turn and swim downstream. Eventually downstream swimming gave way to passive drifting. Hughes' study used only two current speeds (12 cm s^{-1} for juveniles, 5 cm s^{-1} for postlarvae), and it was not clear if the shrimp swam and made headway against the current or at what point shrimp exited from the water column.

Brown and pink shrimp may have the ability to exit from the water column during tidal transport within a few seconds. This ability may be an important aspect of penaeid shrimp ecology if preferred estuarine sediments are patchy in abundance (Rulifson 1981). Data indicate that the behavior used to accomplish this movement is simple and predictable. The rate of descent may be slowed by drifting passively with walking legs extended or be increased by using pleopods for propulsion. Differences in the amount of energy expended for these two generalized methods of descent are assumed. However, even the most expeditious method of exit from the water column can be slow relative to the swiftness of estuarine tidal currents. Thus shrimp may be transported considerable distances (up to hundreds of meters) from the location at which a dive toward the substrate is initiated.

A greater understanding of the processes involved during tidal transport may aid the formulation of habitat management policies. Physical and chemical alterations to estuaries may reduce the ability of penaeid shrimp and other organisms to utilize tides for migration to and from nursery areas. Placement of water intakes and outfalls, dredging, and creation of dredge spoil islands may alter normal migration pathways and reduce the number of estuarine sites available as nursery areas (Rulifson 1980, 1981). Further research is needed to document shrimp responses to the immediate environment during tidal transport.

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SEASONAL AND GEOGRAPHIC DISTRIBUTION OF SEVEN DECAPOD CRUSTACEANS IN APALACHEE BAY, FLORIDA

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ABSTRACT

Seasonal, annual and supra-annual abundance of seven abundant epibenthic decapod macrocrustaceans (shrimp > 3 mm total length, crabs > 3 mm carapace width) collected in Apalachee Bay, Florida, from 1972 to 1979 were investigated. *Pagurus* c.f. *bonairensis, Palaemon floridanus, Tozeuma carolinense, Neopanope texana, Palaemonetes intermedius, Hippolyte pleuracanthus* and *Periclimenes longicaudatus* demonstrated constant seasonal, reproductive and growth patterns during the study period. There were species-specific responses to habitat alterations and climatological variations. Most species' populations decreased in numerical abundance during periods of climatological extremes but increased in concert with benthic macrophytes and drift red algae.

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INTRODUCTION

Among various distributional and taxonomic studies of invertebrates that occur in the Northeast Gulf of Mexico (*e.g.* Wass 1955; Provenzano 1959; Abele 1970; Menzel 1971), few contain life history information and most emphasize areas outside the Gulf (Holthuis 1952; Ryan 1956; Williams 1965; Rouse 1970; Chase 1972; Musick and McEachran 1972; Marsh 1973; Grizzle 1974; Camp, Whiting and Martin 1977; Weinstein, Courtney and Kinch 1977; Cooley 1978).

For the past 10 years, field and laboratory studies have been carried out to compare two river systems that flow into Apalachee Bay, one polluted by kraft mill effluent (Fenholloway), the other unpolluted (Econfina). These studies included analysis of benthic macrophytes (Zimmerman and Livingston 1976, 1979), fish fauna (Livingston 1975), ichthyoplankton (Brady 1981), benthic macrofauna (Stoner 1980a), amphipod abundance and habitat (Stoner 1980b), predator-prey relationships (Stoner 1979; Ryan 1981), and

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trophic organization (Livingston 1980, 1982). Previous studies concerned with epibenthic macroinvertebrate species assemblages in the study area include pre-abatement community structure (Heck 1976; Hooks, Heck and Livingston 1976), diel variation (Greening and Livingston 1982), and species assemblage stability (Dugan and Livingston 1982).

The dominant invertebrates analyzed in the present study are the decapod crustaceans *Pagurus* c. f. *bonairensis, Palaemon floridanus, Tozeuma carolinense, Neopanope texana, Palaemonetes intermedius, Hippolyte pleuracanthus,* and *Periclimenes longicaudatus* (Dugan and Livingston 1982). This study was designed to investigate the seasonal, reproductive and growth patterns of these common crustaceans.

MATERIALS AND METHODS

The study area includes two river drainage systems feeding Apalachee Bay, Florida (Fig. 1).

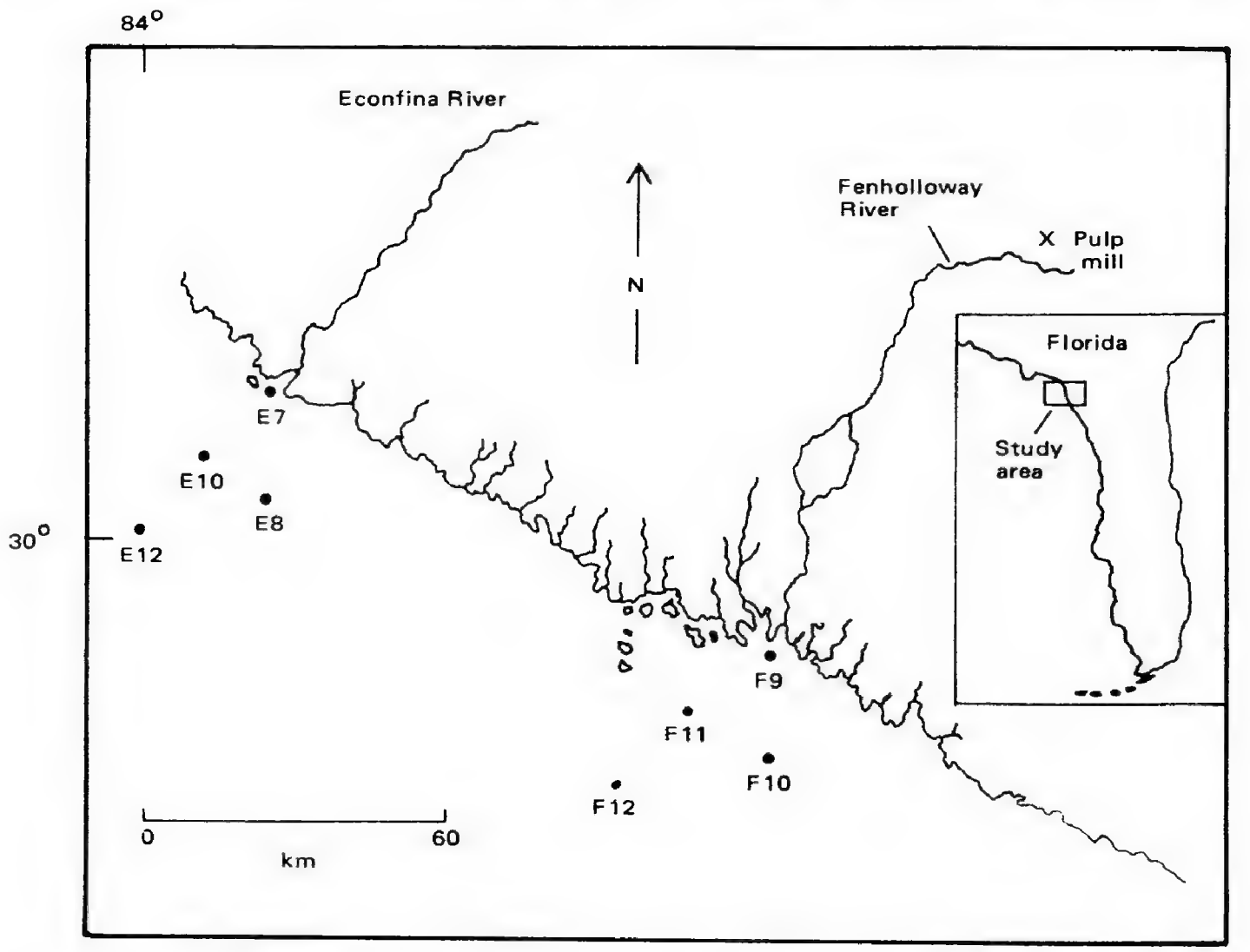

FIG. 1. Apalachee Bay, Florida, with location of permanent sampling stations in the experimental and control offshore areas.

Permanent stations were established to analyze short and long term changes of the dominant invertebrate populations in the Fenholloway offshore area (F9, F10, F11, F12) and its control in the Econfina (E7, E8, E10, E12) (Dugan and Livingston 1982). Stations demonstrated a range of macrophyte biomass from low total standing crop at F9 and F11 (unvegetated stations) to high total standing crop at E8 and E12 (Table 1). Large windrows of red algae *(Digenia simplex,*

TABLE 1

Summary of macrophyte biomass and salinity characteristics at four Econfina and four Fenholloway field sites in Apalachee Bay, Florida, from June 1971 to May 1979. Values are means ± standard deviations (adapted from Stoner and Livingston 1980).

Characteristic	Econfina stations			
	E7	E8	E10	E12
Macrophyte biomass (g dry wt m^{-2})	35±46	402±436	256±196	375±2.9
Salinity (0/00)	17.4±5.2	22.1±4.1	21.9±4.2	25.8±3.3
Range of Salinity (0/00)	0-27.8	11.2-30.0	6.0-31.6	15.0-35.5

Characteristic	Fenholloway stations			
	F9	F10	F11	F12
Macrophyte biomass (g dry wt m^{-2})	0.5±1.1	11.6±18.2	4.3±6.1	106±55
Salinity (0/00)	21.0±4.3	24.6±3.8	24.0±3.7	25.9±3.5
Range of Salinity (0/00)	5.3-31.0	13.0-35.0	9.7-34.4	16.4-33.9

Gracilaria verrucosa, G. folifera and *Laurencia poitei)* were often found in the Econfina offshore area and occasionally in the Fenholloway. The specific source of the drift red algal complex is unknown, but the drift algae are transported by tides and wind. See Livingston (1975) for a detailed description of water quality analysis.

Sampling techniques for collection of the motile epibenthic invertebrates were given by Hooks *et al.* (1976). Seven two-minute trawl-tows were taken at each permanent station on a monthly basis with a 5-m otter trawl (1.9 cm mesh wing and body, 0.6 cm mesh liner) from June, 1972, through May, 1973 and resumed January, 1974, through May, 1979. All invertebrates were taken during the day on an incoming tide. All collections were preserved in 10% buffered formalin solution and invertebrates were later placed in 40% isopropyl alcohol. A ranking technique was used (Fager 1957) to determine the numerically dominant species in each system. This technique reduces bias created by unusually large sporadic increases of individual species. The populations of the seven highest ranked decapod crustaceans were analyzed for monthly and yearly variations in numerical abundance, numbers of ovigerous females, and size distributions. Total lengths (tip of rostrum to end of telson, after Williams 1965) and number of

ovigerous females of the larger shrimp *(Tozeuma carolinense, Palaemon floridanus, Palaemonetes intermedius)* were recorded. These shrimp were ranked by 10-mm increments for length-frequency histograms. Only data on number of ovigerous females were recorded for the smaller shrimp *(Hippolyte pleuracanthus, Periclemenes longicaudatus).* Carapace widths were measured for *Neopanope texana* (after Williams 1965); sex and number of ovigerous females were also noted. Size classes for *N. texana* were in 5-mm increments for males and females separately. Hermit crabs *(Pagurus* c.f. *bonairensis)* were not removed from shells and were therefore only counted.

RESULTS

Ninety-five percent of the macroinvertebrates (116,487 individuals) collected in Apalachee Bay over the seven-year study period were decapod crustaceans. Seven common species comprised 96.1% of the macroinvertebrates collected in the Econfina offshore area (72,925 individuals) and 72.2% in the Fenholloway area (43,562 individuals).

Pagurus c.f. *bonairensis* Schmitt, 1936

Pagurus c.f. *bonairensis* comprised 17.3% (12,601 individuals) of the macroinvertebrates in the Econfina River area and 12.6% (5,488 individuals) in the Fenholloway River area, whereas Hooks *et al.* (1976) reported it to have a relative abundance of 53% in Apalachee Bay. The latter percentage was inflated by the inclusion of empty shells in the enumeration (Hooks, unpub. data), and therefore is not included in the following analysis (June 1971–December 1972). Reduced numbers of *P. bonairensis* occurred at inshore stations (E7, F9) where salinities and biomass of benthic macrophytes and red algae were lowest.

Peak abundances of *P.* c.f. *bonairensis* occurred from November through May in the two drainage systems, and the smallest collections usually occurred in October (Fig. 2). Numerical abundance of *P.* c.f. *bonairensis* over the seven-year study period is given in Fig. 3. Unusually high abundances occurred in the Fenholloway estuary in July and August 1977 and October 1978. Large numbers of these hermit crabs were collected in the Econfina system from October 1978 through the end of the study in May 1979, whereas few were collected in the Fenholloway system in 1979.

Palaemon (Paleander) floridanus Chace, 1942

Heck (1976) and Hooks *et al.* (1976) reported large numbers of *P. floridanus* in Apalachee Bay. Similar numerical abundances in the Econfina and Fenholloway offshore areas (15.8% and 12.0%, respectively) occurred during the present study. The greatest numbers of *P. floridanus* occurred at stations predominately vegetated by red algae (E8, E10, F11) (Hooks *et al.* 1976; H. S. Greening, University of Georgia, personal communication; Dugan and Livingston 1982).

Seasonal peak abundances occurred during December and January over the seven-year sampling period in both river systems (Fig. 2). Minimum

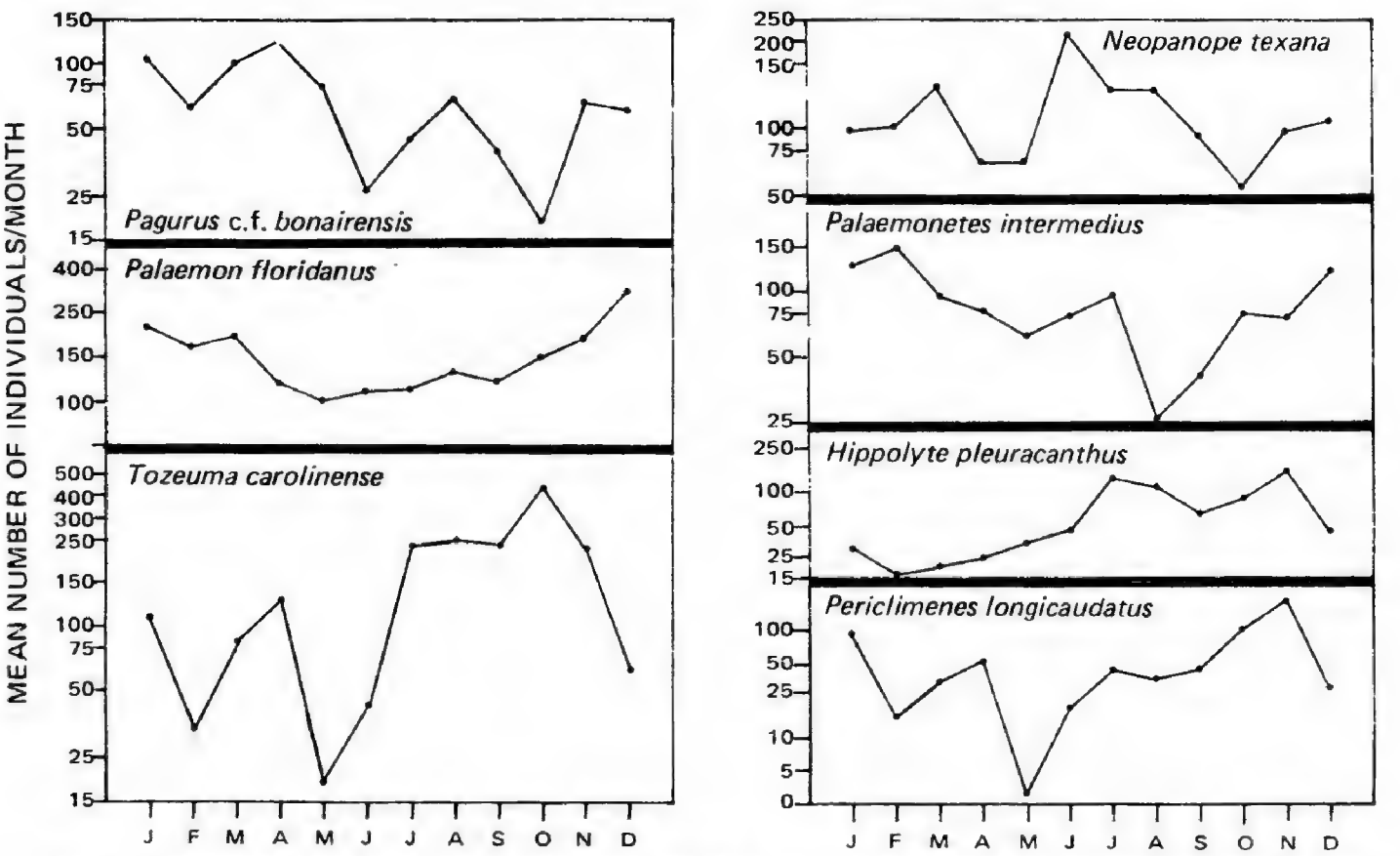

FIG. 2. Seasonal abundance of seven dominant decapod crustacean species in Apalachee Bay, Florida. Each value is a geometric mean (Musick and McEachran 1972) for monthly collections from all eight stations.

numbers occurred from April through September. *Palaemon floridanus* maintained large populations in the Econfina throughout the study (Fig. 3) except during two periods of climatological extremes. The first population collapse followed heavy rains in April, 1973, when salinities were greatly reduced (Zimmerman and Livingston 1976). Macrophyte biomass declined as a result of the salinity reduction (Livingston 1980). Subsequently, these macrophytes have recovered. Moreover, numbers of shrimp collected increased from 1974 until the winter of 1976–77 when they decreased concurrent with extreme low winter temperatures of January 1977. The Fenholloway system did not have large populations of *P. floridanus* prior to pollution abatement in 1974. Following the abatement program, the numbers of *P. floridanus* in the Fenholloway increased until 1978.

Monthly size class frequencies were constant over the sampling period (Fig. 4). The total lengths *(tl)* ranged from 9 to 49 mm. Ovigerous shrimp were found from April to October, with maximum number of gravid females occurring in April and August. Sizes ranged from 25 to 35 mm *tl*; the majority exceeded 30 mm. Large proportions of small (10–19 mm) individuals occurred in February (35% of the population) and June (50%). The greatest proportion of large shrimp (> 30 mm) occurred from March through May.

Tozeuma carolinense Kingsley, 1978

Tozeuma carolinense comprised 21.7% (15,837 individuals) of the total macroinvertebrate catch in the Econfina area and only 7.8% (3,298 individu-

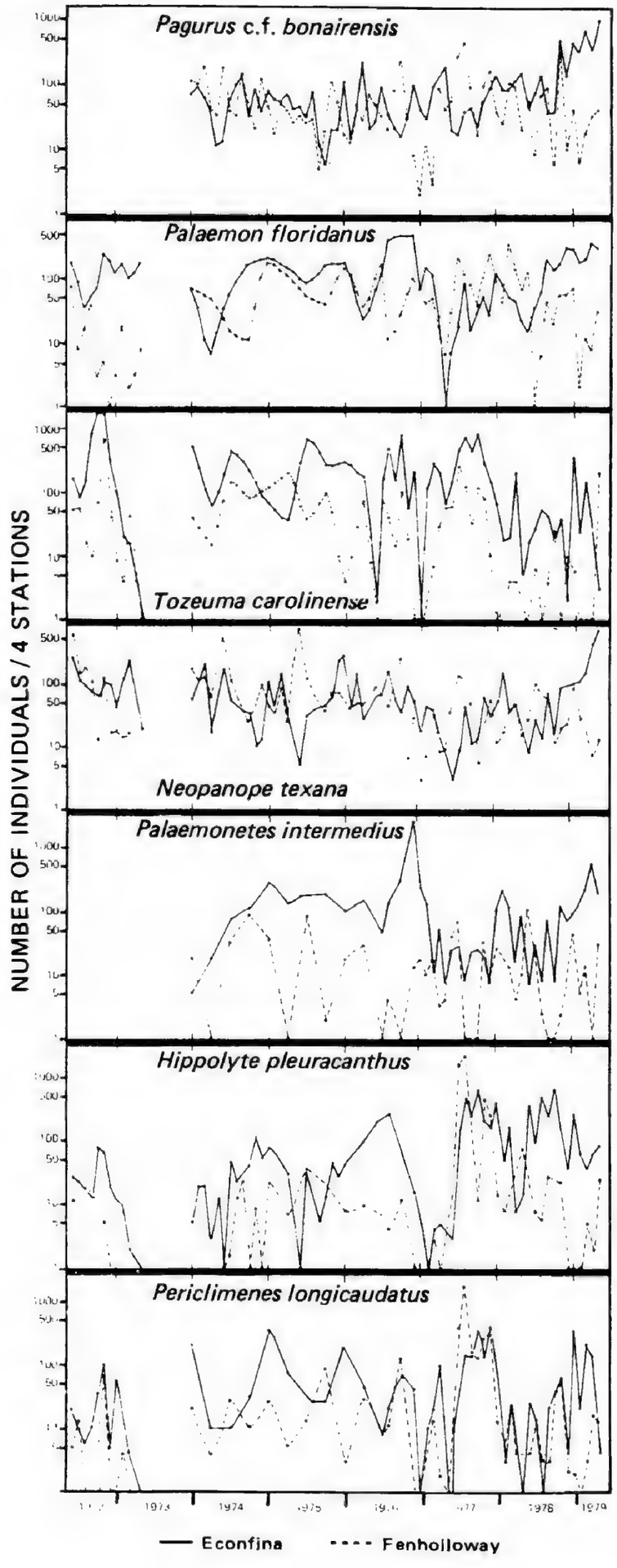

FIG. 3. Geometric mean (Musick and McEachran 1972) of numbers of individuals of seven dominant decapod crustaceans collected monthly from 1972 to 1979 in Apalachee Bay, Florida. Solid line = Econfina, dotted line = Fenholloway. (a) *Pagurus* c.f. *bonairensis*, (b) *Palaemon floridanus*, (c) *Tozeuma carolinense*, (d) *Neopanope texana*, (e) *Palaemonetes intermedius* (f) *Hippolyte pleuracanthus*, (g) *Periclimenes longicaudatus*.

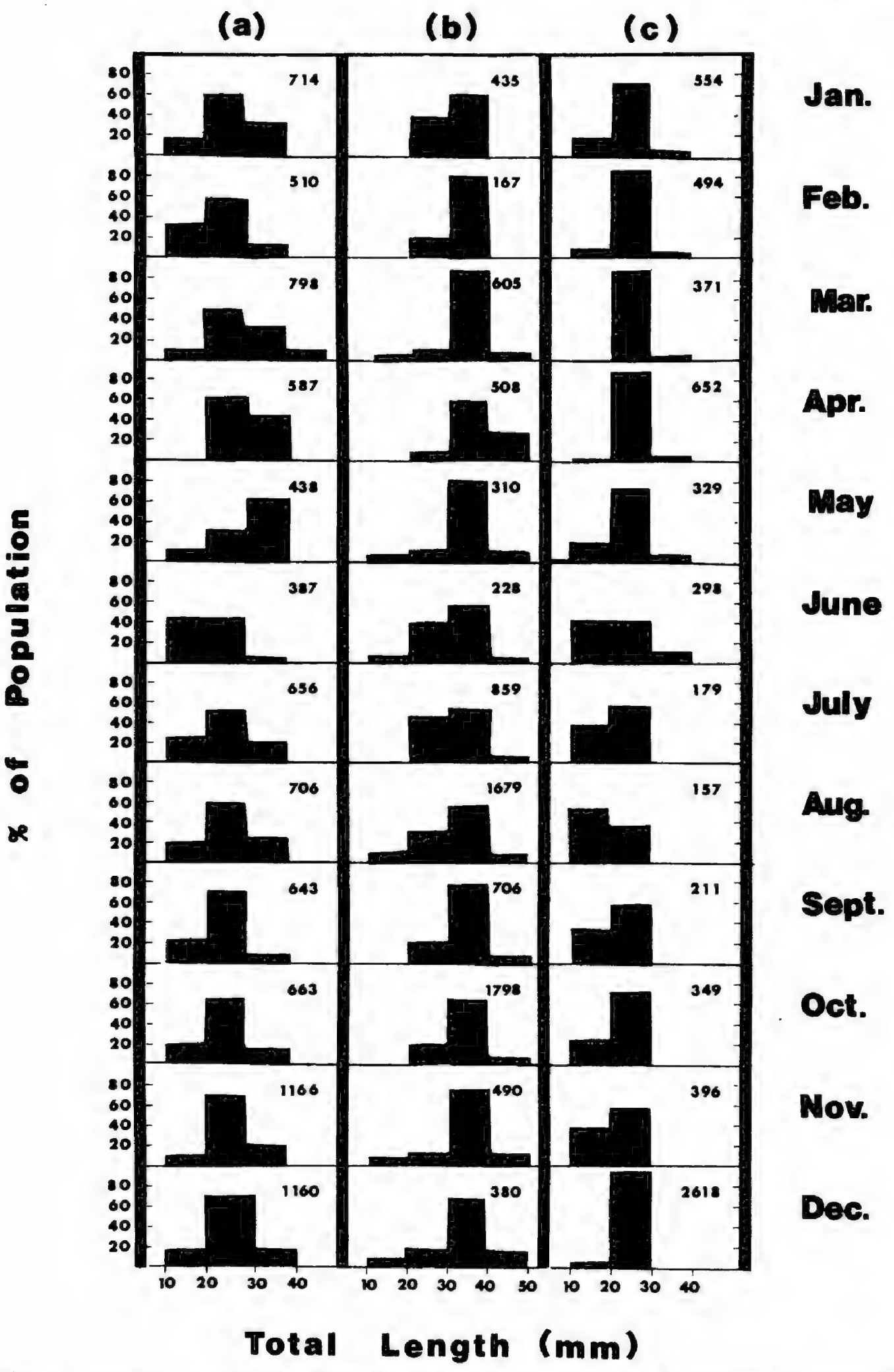

FIG. 4. Average monthly size class frequency for (a) *Palaemon floridanus*, (b) *Tozeuma carolinense*, and (c) *Palaemonetes intermedius* collected from 1976 to 1979 in Apalachee Bay, Florida.

als) in the Fenholloway system. *Tozeuma* was most abundant at stations dominated by *Thalassia testudinum* and *Syringodium filiforme* (E12, F12). Few such shrimp were found in areas of low salinity and sparse vegetation (E7, F9, F11). In both offshore areas, peak abundance of *T. carolinense* occurred from July through November (Fig. 2). Minimum abundance occurred during February, May, and June. Catch abundance over the seven-year period is given in Fig. 3.

Tozeuma carolinense ranged in size in this study from 13 to 54 mm total length (Fig. 4). Fifty percent or more of the shrimp measured 30–39 mm *tl* each month. Gravid females first appeared in February; in early spring most shrimp > 35 mm were ovigerous and all > 40 mm were ovigerous. Ovigerous females were predominant in catches from Apalachee Bay in early spring and late summer, but no ovigerous individuals were found from October through February.

Neopanope texana (Stimpson, 1859)

Neopanope texana was the most abundant xanthid crab collected in Apalachee Bay. Collections totaled 6,247 individuals (8.6% of macroinvertebrates) in the Econfina area and 6,440 individuals (14.8%) in the Fenholloway estuary. Most individuals of *N. texana* occurred at stations where red algae frequently occurred (E8, E10) (Dugan and Livingston 1982); few individuals occurred at stations farthest from shore (E12, F12). Seasonal peaks occurred in March and June, and minimum numbers were collected in April, May, and October (Fig. 2). Two notable abundance peaks of *N. texana* occurred in Apalachee Bay. High numbers in the Fenholloway drainage area were collected in trawls with high biomass of the red algal complex at F10 and F11 July through September 1972 (Fig. 3). Collections were small in both systems in 1977 and 1978. During March through May 1979 there was considerable recruitment of small individuals (< 4 mm) which were captured in large masses of red drift algae at stations E8 and E10.

The ratio of male to female *N. texana* was 1:1 in Apalachee Bay. Males ranged from 3 to 28 mm carapace width *(cw)* (1,980 individuals) while females measured from 3 to 22 mm (2,046 individuals). Monthly size/class distribution showed an influx of juveniles in Apalachee Bay in spring, although the small size class was present all year (Fig. 5). Frequency of the < 6 mm size class in May (77%) shifted to the 6–10 mm size class over the following three months. Subsequently, the size distribution shifted as larger crabs were more abundant through the winter. In these large size classes, the sex ratio was not 1:1. Males comprised 75% of the 11–15 mm size class from May to November whereas females predominated (65%) from December to April. This asymmetrical distribution was more pronounced in crabs > 16 mm *cw* in which males outnumbered females all year, contributing 95% from April to October and 60% from December to March.

Ovigerous females occurred from March through November and measured 5 to 18 mm *cw* (Fig. 5). The number of ovigerous females peaked in

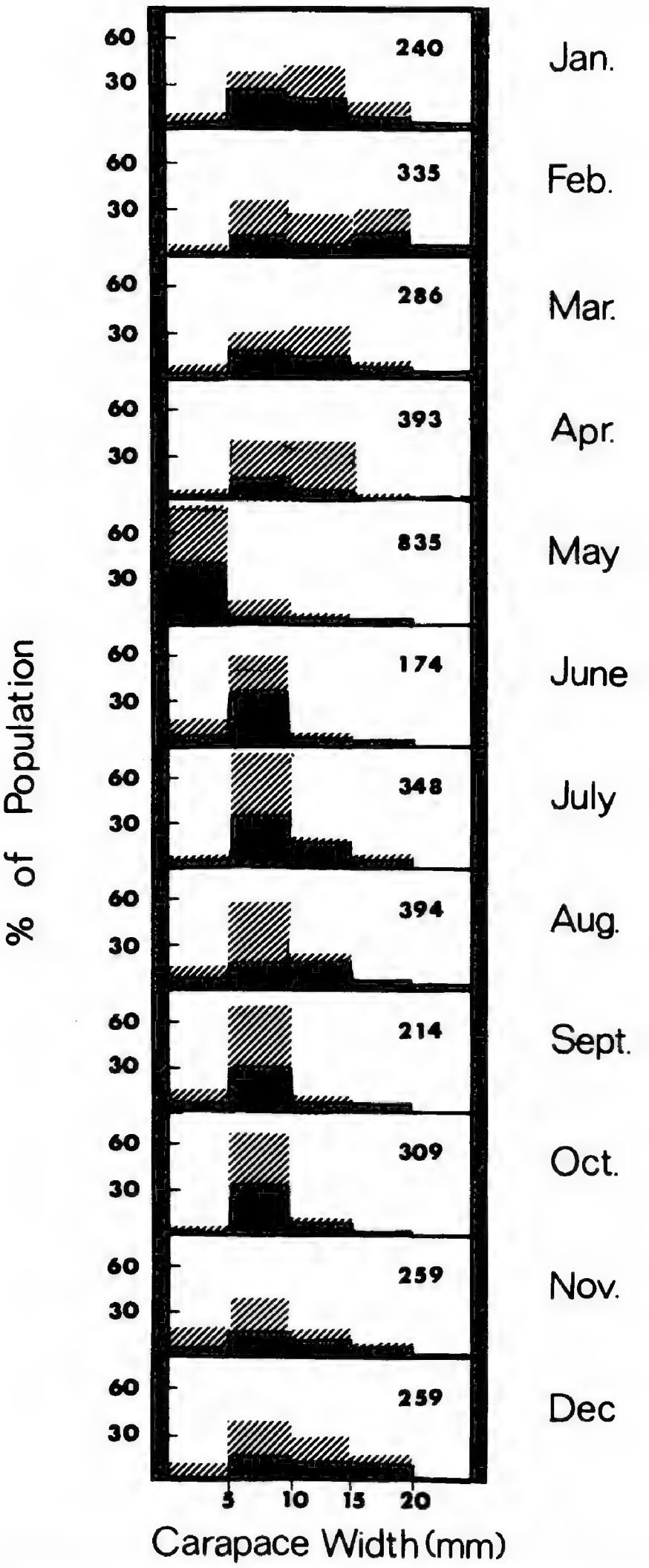

FIG. 5. Average monthly size class frequency for *Neopanope texana*, with distribution of males (solid black) and females (diagonal stripes) within size-class categories collected from 1976 to 1979 in Apalachee Bay, Florida.

spring and late summer. The mean carapace width of ovigerous females in spring was 12.7 mm while mean size of those ovigerous in summer was 8.2 mm.

Palaemonetes (Palaemonetes) intermedius Holthuis, 1949

Abele (1970) found *Palaemonetes intermedius* uncommon in northwest Florida; however, it was the most common caridean shrimp at inshore stations at Crystal River, Florida (Lyons *et al.* 1971). *Palaemonetes intermedius* was relatively common in Apalachee Bay; it ranked fifth in abundance in both offshore areas. This species comprised 16.5% of the catch (12,052 individuals) in the Econfina system and 2.5% (1,103 individuals) in the Fenholloway area. It was abundant only in areas of low salinity (E7, F9). Winter peaks occurred (Fig. 2) and minimum numbers of *P. intermedius* were found in August. Low numbers recorded in 1972–73 were a result of a taxonomic discrepancy when Hooks *et al.* (1976) may have misidentified *P. intermedius* as *P. vulgaris* (K. L. Heck, Jr., Academy of Natural Sciences of Philadelphia, personal communication); therefore, data from these years were not used in population analyses. A large peak in the Econfina estuary occurred in December 1976 when 2,411 individuals were captured at E7 (Fig. 3).

All *P. intermedius* ranged from 9 to 42 mm total length. Large proportions of the 10–19 mm size class appeared in summer (Fig. 4). The 20–29 mm size class reached maximum proportions in autumn. This size class continued to dominate throughout the spring until the first recruitment of new offspring. In Apalachee Bay ovigerous *P. intermedius* occurred from March through October with a few appearing in February. Two peaks of ovigerous females were noted; the largest females spawned in the first peak and were gradually replaced by smaller individuals in the second peak. These findings are similar to those noted by Wood (1967) for *P. pugio.* Ovigerous specimens collected in Apalachee Bay were 22 to 33 mm *tl.*

Hippolyte pleuracanthus (Stimpson, 1871)

Confusion exists concerning the nomenclature of the species of *Hippolyte* found in the northeast Gulf of Mexico (Chace 1972, Shield 1978, Gore *et al.* 1981). According to Gore *et al.* (1981) and Abele (Florida State University, personal communication) the correct name to use is *Hippolyte pleurancanthus* and not *H. zostericola* until the nomenclatural status is settled. This seagrass-dependent species occurred in large numbers in Apalachee Bay, comprising 9.0% (6,528 individuals) in the Econfina and 12.8% (5,570 individuals) in the Fenholloway system. The majority of individuals were caught at stations characterized by drift red algae (Dugan and Livingston 1982).

Abundance of *H. pleuracanthus* peaked from July through November and coincided with peak macrophyte biomass. Minimum numbers occurred from February through April (Fig. 2). Unusually high numbers were taken in July and August 1977, during periods of high red algal density. Abundances

increased in the Econfina system from 1972 to 1977, with decreasing numbers following the peak in October 1977. *Hippolyte pleuracanthus* did not follow the same trend in the Fenholloway system. Numbers remained low throughout the period of study in the Fenholloway estuary except for the peaks in the summer of 1977.

Ovigerous females occurred year-round and ranged from 8 to 21 mm *tl.* However, during winter months only shrimp measuring > 12 mm were ovigerous. Ovigerous females measuring < 10 mm were not collected until June. All *H. pleuracanthus* captured were 5 to 21 mm *tl.* Smaller individuals (< 9 mm *tl)* were common during June and winter months.

Periclimenes (Periclimenes) longicaudatus (Stimpson, 1860)

Weinstein *et al.* (1977) found *P. longicaudatus* associated with *Thalassia* habitats in southwest Florida as did Abele (1970) in northwest Florida. This species occurred in considerable numbers at outer Apalachee Bay stations; it contributed 7.3% of the catch (5,324 individuals) in the Econfina offshore area and 10.0% (4,346 individuals) in the Fenholloway. Peak abundance occurred in November and minimum numbers were collected in May (Fig. 2). There were no discernable trends of increasing or decreasing abundances in either system (Fig. 3). Exceptionally high abundances occurred in both systems in the summer of 1977 (similar to the increased abundances of *H. pleuracanthus).*

Periclimenes ranged in size from 5 to 22 mm *tl,* with ovigerous shrimp measuring 9 to 22 mm. Few ovigerous shrimp were found, and these occurred from February to October.

DISCUSSION

Predation, habitat structure, and reproduction can all be expected to contribute to seasonal population pulses of the decapod crustaceans studied. This study was not designed to isolate causative factors for population variations but to determine baseline population trends of dominant species.

Numerous studies in Apalachee Bay have indicated the importance of crustaceans as a primary food source for fishes (Stoner 1979, 1980a; Ryan 1981; Greening and Livingston 1982). Predation is also related to habitat complexity. Increased habitat complexity, defined as above-ground plant biomass (Heck and Wetstone 1977) or seagrass structure (Coen *et al.* 1981), creates a refuge from predators; therefore, seasonal increases in seagrass biomass may contribute to decreased foraging efficiency for some fish species.

Ovigerous females were captured from March through October in all species *(Hippolyte pleuacanthus* was ovigerous year round). Stoner (1980b) obtained similar results for Apalachee Bay amphipods. He attributed this seasonality to water temperature; 15°C was the critical water temperature for onset of reproductive activity. The mean size of gravid shrimp diminished in late spring and summer. Fish predation has been shown to cause

size shifts during summer months in amphipod populations (Nelson 1980). Reduced minimum size of reproductive females in amphipods (Nelson 1980) and shrimp (Wood 1967) has been reported in summer. In the present study, decreased mean size of the total population and gravid females occurred during summer months for *Palaemon floridanus, Tozeuma carolinense, Neopanope texana,* and *Palaemonetes intermedius.*

Two patterns of seasonal abundance peaks emerged in the species studied. *Pagurus* c.f. *bonairensis, Palaemon floridanus* and *Palaemonetes intermedius* had peak populations in winter through early spring, when fish populations and seagrass biomass were minimal (Livingston 1975; Zimmerman and Livingston 1976). Reproductive activity ceased in October in palaemonid shrimp; therefore other factors such as reduced predation must contribute to their increased numbers during the winter. No reproductive information was collected on *Pagurus* c.f. *bonairensis;* therefore no conclusions can be drawn concerning factors contributing to their seasonal pattern.

Tozeuma carolinense, Hippolyte pleuracanthus and *Periclimenes longicaudatus* had peak populations during summer and fall months, whereas *Neopanope texana* was collected in peak numbers only in summer. These large populations concurred with periods of reproductive activity, high predation pressure, and increased seagrass biomass. The three shrimp species have been closely associated with seagrass in other studies (Ewald 1969, Abele 1970, Rouse 1970, Grizzel 1974, Weinstein *et al.* 1977).

Dramatic changes in individual species collections occurred episodically over the study period. In general, the availability of long-term data facilitated recognition of non-seasonal peaks and depressions which could be correlated with alterations in available habitat. Populations of all common species (except *Palaemonetes intermedius,* which increased) were depressed during periods of low salinity following the heavy rains in April, 1973, and low winter temperatures in 1976–77. Livingston (1975) also found reduced numbers of fish species associated with reduced salinities in the spring of 1973. Macrophyte biomass declined as a result of the salinity reduction (Livingston 1980).

Drift red algae may have contributed to episodic peaks of most species. *Pagurus* c.f. *bonairensis, Palaemon floridanus, Neopanope texana, Hippolyte pleuracanthus,* and *Periclimenes longicaudatus* were all collected in large numbers when red algal biomass was high. Occurrence of this algal complex is unpredictable and erratic. Stoner and Livingston (1980) attributed occurrence of red algal windrows to winter storms. One consideration is that the increased decapod populations were due to entrapment in the complex algal structure during collection. Other studies have found these species' populations to be greatly influenced by red algal biomass (Hooks *et al.* 1976; Thorhaug and Roessler 1977; Coen *et al.* 1981; Gore *et al.* 1981; Dugan and Livingston 1982; Greening and Livingston 1982).

Dynamics of the seasonal and long-term distributions of these common crustaceans are multidimensional and cannot be attributed to simple

environmental functions. While predation may be important, climatological impacts such as atypical temperature and salinity patterns, in particular their seasonal and long-term effect on macrophyte standing crop, also appear to be critical to an understanding of variation in population distribution. The role of benthic macrophytes and drift red algal complex in mediating predation deserves further attention as does the natural history of dominant invertebrate populations and their predators. Experimental work aimed at delineating the importance of these environmental factors in seagrass beds is needed to understand the mechanisms of population dynamics. Without such information, it is unlikely that specific hypotheses can be developed and tested experimentally in a uniform and meaningful way.

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OPTIMUM SALINITY REGIME FOR OYSTER PRODUCTION ON LOUISIANA'S STATE SEED GROUNDS

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ABSTRACT

Salinity, spatfall, and seed oyster production data from three stations on Louisiana's prime seed grounds were collected from 1971–1981. Examination of the relationships between each of the variables revealed that salinity during the year in which spatfall occurred was closely related to the production of seed oysters in the ensuing year. The optimum annual salinity regime was derived from all of the year/station regimes which were associated with good seed production (>20 oysters/m^2). The relationship between the optimum regime and seed production was expressed with the regression equation: Seed production = −43.89 + 2144.5 (Σ monthly deviations from the optimum regime^{-1}). The critical months within the optimum annual regime appear to be May through September. Optimum May salinities are from 6–8 ppt. Salinities should average 13 ppt in June and July and not increase to greater than 15 ppt until late August. September salinities should not average more than 20 ppt.

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INTRODUCTION

The Louisiana oyster *Crassostrea virginica* (Gmelin) industry relies heavily upon seed oysters produced on state-controlled seed grounds. Historically, the most productive of these grounds has been an area east of the Mississippi River of approximately 200,000 acres (Mackin and Hopkins 1961). Man-induced perturbations, such as levee construction and channelization, coupled with the natural processes of deltaic decline have resulted in steadily increasing salinities over the entire grounds (Gagliano, Meyer-Arendt and Wicker 1981). Coincident with increasing salinities has been a decrease in the size of the area producing seed oysters. Several researchers have reported that the decreased area is in fact a result of the increased salinities (Gunter 1953, Pollard 1973, Dugas 1977).

In an attempt to reverse the landward salinity intrusion and thereby re-establish formerly productive reefs, a number of structures designed to divert Mississippi River water to the area of the seed grounds have been constructed or are now being planned. The most efficient structure envisioned to date would theoretically shift the 15 ppt mean isohaline to pre-1950 locations for nine out of every ten years (U.S. Army Corps of Engineers, New Orleans District 1970). Maintenance of this line is expected to increase seed oyster production dramatically.

Fifteen ppt was chosen (Theodore B. Ford, Louisiana Department of Wildlife and Fisheries, personal communication) primarily due to the inability of the oyster drill, *Thais haemastoma canaliculata* (Gray), to flourish in waters less than 15 ppt (Butler 1954, Chapman 1959). However, Gunter (1955) stated there are several organisms, in addition to the oyster drill, whose abundance is salinity dependent and which limit oyster production. These include predators such as portunid and xanthid crabs, predaceous polychaetes, boring gastropods, and fouling organisms which inhibit oyster set such as boring and encrusting sponges, barnacles, bryozoans and algae. If these organisms, along with other salinity dependent factors such as gametogenesis (Butler 1949) and larval survival (Davis 1958), play an important role in seed oyster production, then maintenance of the 15 ppt mean isohaline may not be the most judicious use of the diversion potential.

Determination of the optimum salinity or salinity regime for seed oyster production in Louisiana could conceivably be accomplished by incorporating each of the variables governing production and their individual responses to salinity. A more direct approach, however, would be to examine the relationship between salinity and seed oyster production for a number of years in which production ranged from good to bad. The purpose of this report is to determine the optimum annual salinity regime, using historical data, for the production of seed oysters on Louisiana's seed grounds.

AREA DESCRIPTION AND HYDROLOGY

The state's prime seed grounds lie in the deltaic plain of the Mississippi River in southeastern Louisiana (Fig. 1). The area is bordered on the west and south by the Mississippi River, on the north by Bayou Terre aux Bouefs (an abandoned distributary of the Mississippi), and on the east by Breton Sound.

Since the virtual completion of the Mississippi's levee system from New Orleans to Baptiste Collette Bayou, alluviation in this area from overbank flooding has been minimal. As a result, the area is presently in a state of decline characterized by subsidence and erosion with land masses slowly being replaced by shallow bay systems (Gagliano *et al.* 1981).

Salinities in the area generally increase from the interior marshes to the open bays at times when local rainfall dominates the freshwater input. However, when the Mississippi or Pearl rivers are at a high stage, freshwater or freshened seawater often enters the area from the open waters of Breton Sound. The Bonnet Carre Spillway, a flood control structure of the Mississippi which drains into Lake Pontchartrain, has the potential to greatly reduce salinities on the seed grounds but the structure has been used only seven times since its construction in 1935. There are also three diversion structures located at Bellair, Bohemia and Bayou Lamoque which supply river water to the area. These have a relatively small and localized effect on seed ground

FIG. 1. Prime seed oyster producing area of southeastern Louisiana with pertinent hydrological influences.

salinities due to their position and their limited capacities. A proposed diversion structure at Caernarvon will have a much larger dilution capability due to the vast expanse of marsh acting as a freshwater reservoir between the structure and the seed grounds (U.S. Army Corps of Engineers, New Orleans District 1982).

METHODS

Salinity, spatfall and seed oyster production data were collected over an approximate 10-year period from April 1971 to September 1981 from three areas within Louisiana's prime seed grounds. We have designated the areas Black Bay, Bay Gardene and California Bay (Fig. 2).

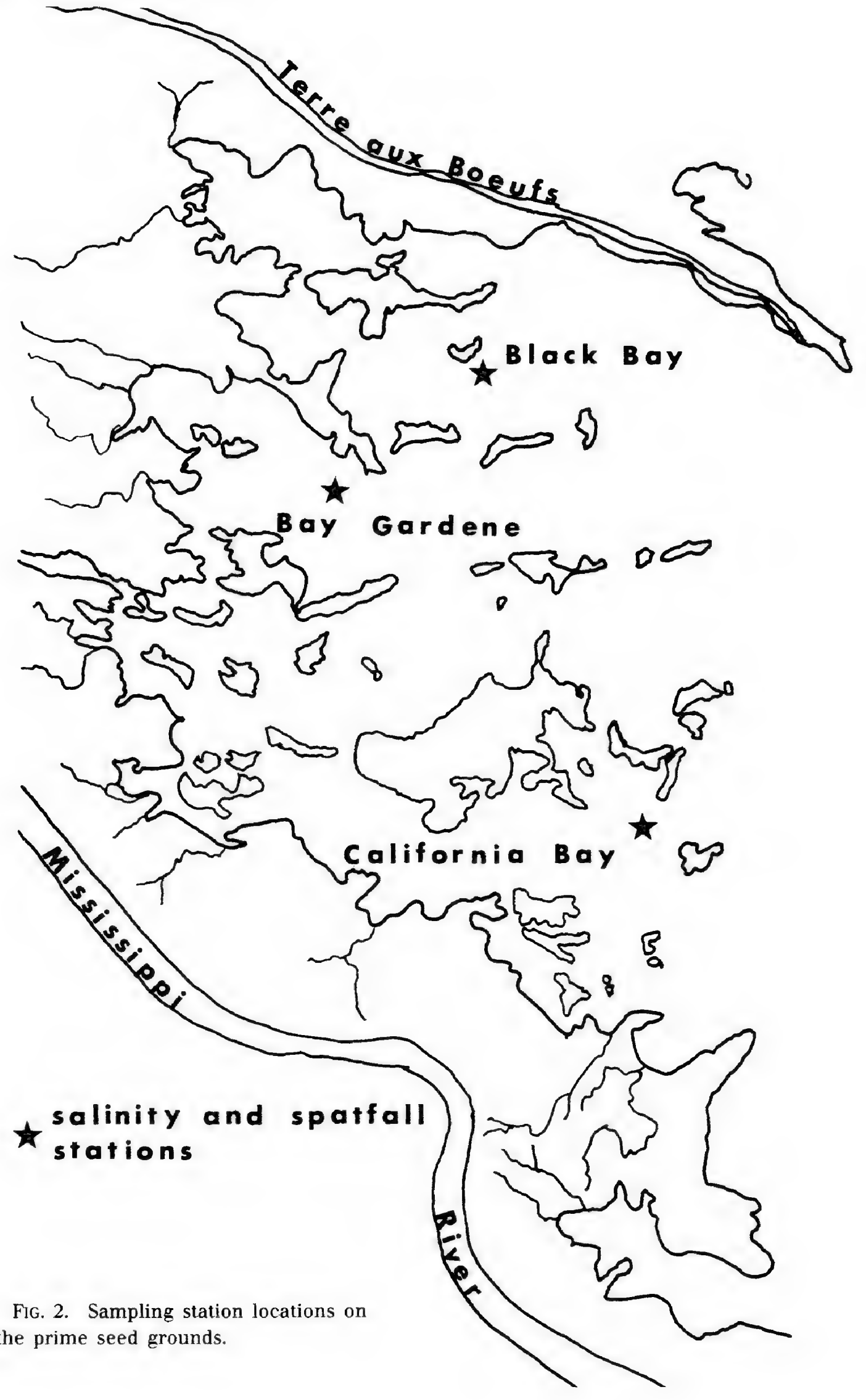

FIG. 2. Sampling station locations on the prime seed grounds.

Salinity was recorded weekly at a permanent station within each of the three areas. Spatfall was measured by use of 10 x 10 cm collecting plates modified from Butler (1955). The plates were deployed weekly in each area adjacent to the salinity stations. Upon retrieval, spat were counted and mean spat/cm^2 was calculated. We have assumed that setting intensities on the collecting plates were a reliable index of the available set.

Seed oyster production was determined by the random square meter method using SCUBA (May 1972). An average of five replicate samples was taken in June or July in each of the three areas from 1974–1981. In general, the same reefs were sampled each year even though the precise sampling sites may have been different. The oysters were separated into size groups of 1–25 mm, 26–50 mm, 51–75 mm, and >75 mm. Oysters 26–75 mm in height were designated as seed oysters. According to St. Amant (1958), most Louisiana oysters in this size range are from 7–14 months old. Therefore, seed oysters sampled in June–July probably set from April to October during the preceding year. An average of 20 seed oysters/m^2 on the reefs of the public ground is required to satisfy the minimum requirements of the fishery. Therefore, we identified seed production data above and below 20 seed oysters/m^2 as "good" or "poor" production, respectively.

RESULTS AND DISCUSSION

A wide range of mean annual salinities (10.7 to 23.0 ppt) and seed oyster production (0.7 to 224.3 oys./m^2) was observed during the period studied. In order to construct the optimum salinity regime for seed production we sought to identify the relationships between salinity and set, set and seed production, and salinity and seed production.

SET *VS.* SALINITY

Over 85% of the setting which occurred at the three stations from 1971–1980 took place in June through September. For this reason we chose these four months, hereafter referred to as "summer", in our comparison of set and salinity. The mean summer set per spat collector in 2 ppt intervals is shown in Figure 3. Approximately 400 set/salinity values are represented.

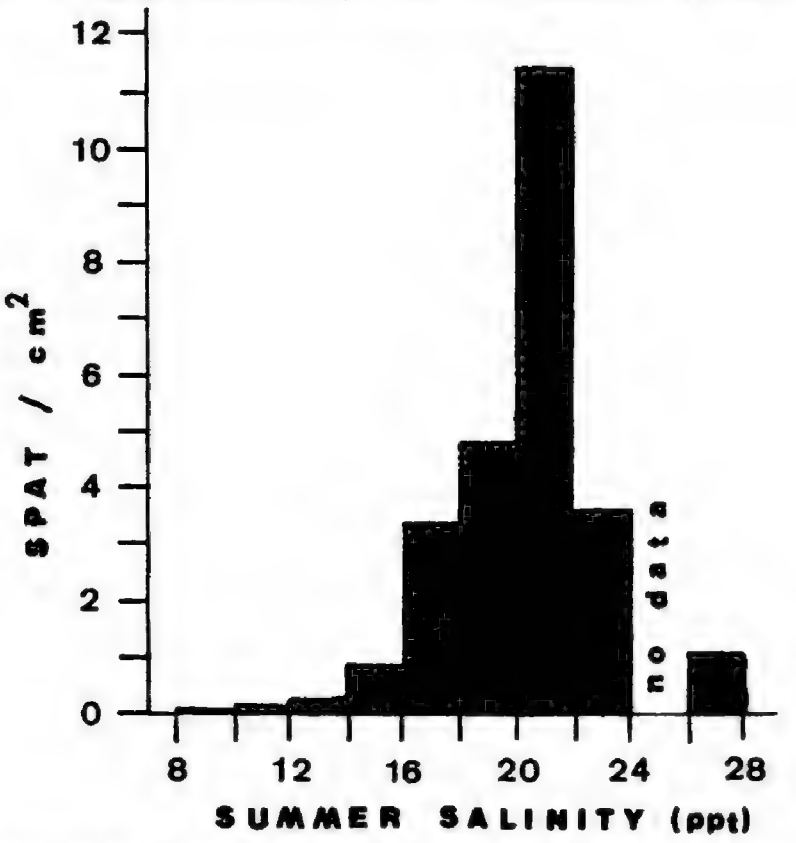

FIG. 3. Mean setting intensities *versus* corresponding mean summer salinities.

Virtually no setting took place when mean summer salinity was less than 10 ppt (Table 1). Setting intensities were minimal (<0.1 spat/cm²) from 10–

TABLE 1

Salinity, set, and seed production values for each area, 1971–1981.

Year	Mean Summer* Salinity (ppt)	Mean Summer* Set (spat/cm²)	Seed Production (oysters/m²)
		Black Bay	
1971	18.4	4.3	---
72	18.7	9.3	---
73	15.1	2.4	---
74	19.4	1.6	43.3
75	16.7	7.0	5.2
76	20.2	18.9	9.7
77	23.3	3.3	4.6
78	11.3	0.0	4.0
79	14.4	0.4	0.8
80	21.1	5.6	224.3
81	---	---	16.4
		Bay Gardene	
1971	16.5	1.4	---
72	18.5	4.9	---
73	12.2	0.2	---
74	16.7	0.4	39.0
75	14.8	0.5	11.2
76	17.4	5.2	29.2
77	23.1	3.3	32.4
78	9.1	0.0	9.2
79	12.5	0.3	2.3
80	18.8	5.0	23.1
81	---	---	12.3
		California Bay	
1971	21.1	8.2	---
72	19.5	5.8	---
73	14.6	0.5	---
74	18.3	2.0	35.0
75	21.5	7.0	4.9
76	20.5	15.7	1.9
77	27.1	1.2	1.1
78	11.7	0.1	2.8
79	14.6	0.4	0.7
80	24.1	5.8	24.4
81	---	---	5.4

*Summer = June, July, August and September

12 ppt. At summer salinities of 12–16 ppt, setting increased to approximately 1.0 spat/cm². From 16–22 ppt setting intensity was consistently high with a peak occurring between 20 and 22 ppt. Setting intensity decreased substantially above 22 ppt but remained higher than the intensities observed at less than 16 ppt.

May and Bland (1970) also found greater setting intensities associated with higher salinities. Possible explanations of this relationship include suppressed gametogenesis (Butler 1949, Davis and Calabrese 1964) and reduced larval survival (Davis 1958, Calabrese and Davis 1970) at lower salinities.

PRODUCTION *VS.* SET

In comparing seed production and set we assumed a lag of approximately one year between set and seed oysters. The years with heavy sets were followed by years of poor seed production. Likewise, the lighter sets often resulted in better production (Fig. 4, Table 1). An inverse relationship between production and set was also noted by Webster and Shaw (1968) on the eastern shore of the Chesapeake Bay.

An exception to this relationship was seen for the three lightest setting intensities. In these cases mean summer salinities of less than 12 ppt

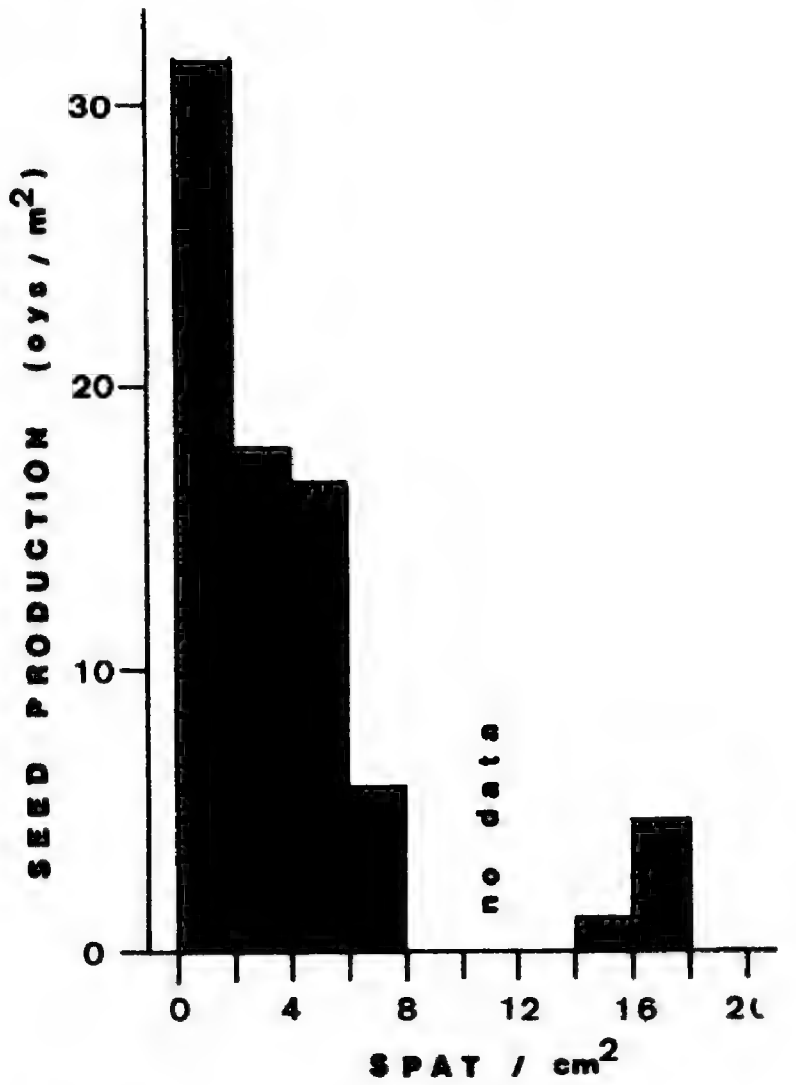

FIG. 4. Seed oyster production *versus* corresponding setting intensities of the preceding year. Poor production for the lowest setting intensities (<0.1 spat/cm²) is obscured by the 0–2 spat/cm² interval.

apparently reduced setting (<0.1 spat/cm²) to the extent that production was limited. These values were obscured in Figure 4 due to their inclusion in the 0–2 spat/cm² interval.

Good seed production resulted from setting intensities as low as 0.2 spat/cm². Therefore, sets of 0.2 spat/cm² or greater were apparently sufficient for good seed production. If production was poor despite sufficient setting, as was more often the case, then other limiting factor(s) were responsible.

PRODUCTION *VS.* SALINITY

The relationship between mean summer salinities at setting and seed production in the ensuing year for all three stations (1973–81) is shown in Figure 5. A fairly narrow range of salinities (12.2–17.4 ppt) was associated with good seed production (Table 1). On either side of the range, production was severely restricted. Poor production for the low salinities (<12.2 ppt) was associated with minimal set. Since setting was sufficient at the high salinities (>17.4 ppt), it appears that the resultant poor production was due to other salinity dependent factors.

Gunter (1955) offers possible identification of these factors. He found a direct relationship between high salinities and high oyster mortalities. He attributed these mortalities to the increased abundance of oyster predators associated with the high salinities.

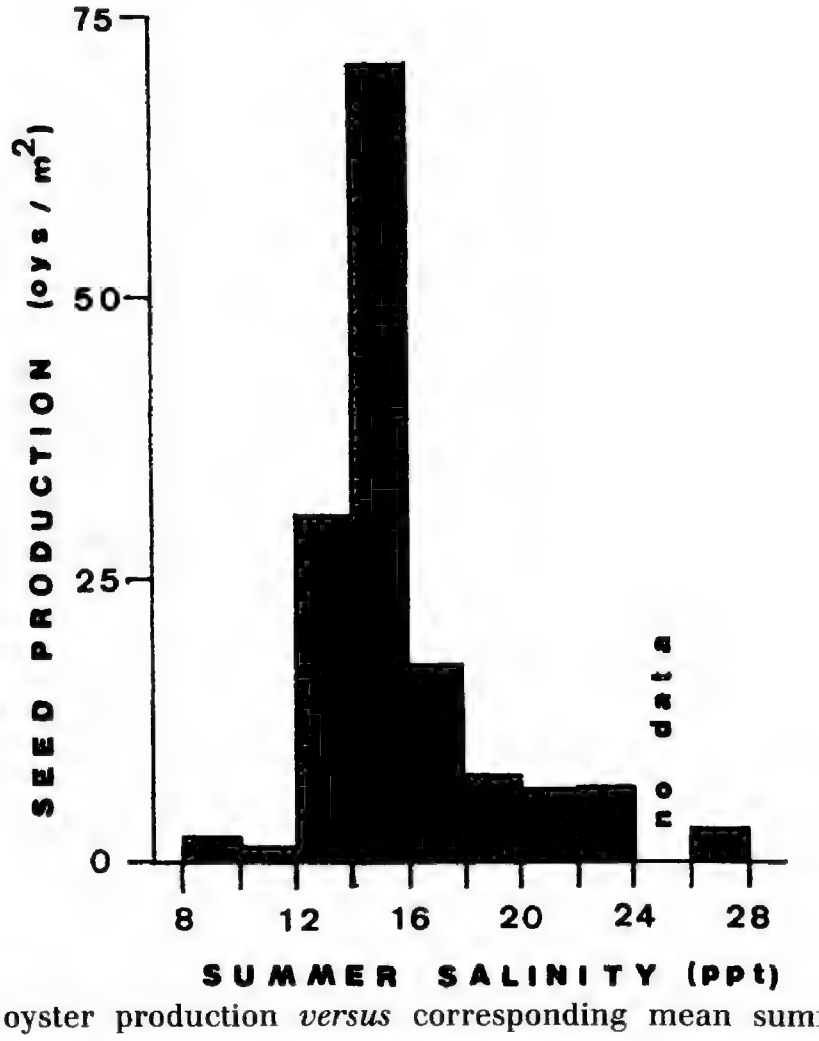

FIG. 5. Seed oyster production *versus* corresponding mean summer salinities of the preceding year.

OPTIMUM REGIME

In the preceding discussions we have used mean summer salinities in the comparisons with set and production. Mean values are helpful in demonstrating general associations but from a practical standpoint (*i.e.*, freshwater diversion) a monthly salinity regime for the entire year is needed. Towards this end, we plotted salinity regimes by month for each year at each station—a total of 24 year/station regimes. There was a remarkable similarity among the eight year/station regimes which were followed in the ensuing year by good seed oyster production. Consequently, we theorized that a composite or mean regime of these eight would approach the optimum for seed production (Fig. 6). To test this theory we took the sum of the monthly salinity deviations in ppt from the composite, for each of the eight regimes, and plotted these deviations versus the corresponding seed

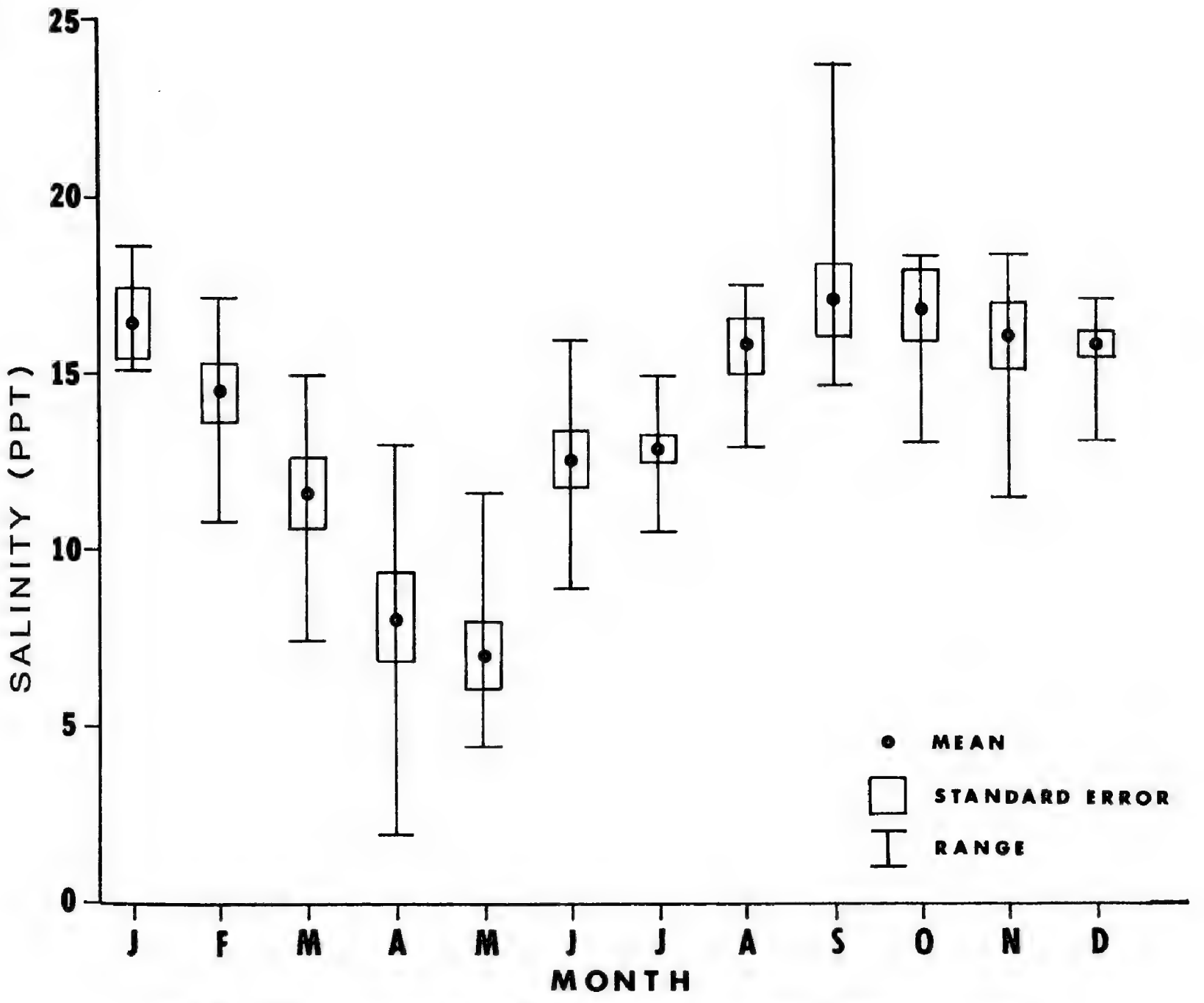

FIG. 6. Derived optimum annual salinity regime for seed oyster production.

production. As expected, seed production decreased as the deviation from the composite increased (Fig. 7). The equation expressing this relationship is:

$$\text{Seed production} = -103.827 + 3299.23\ (\Sigma \text{ monthly deviations}^{-1})$$
$$\text{with } R^2 = 0.81;\ F = 25.9,\ p < 0.01;\ n = 8.$$

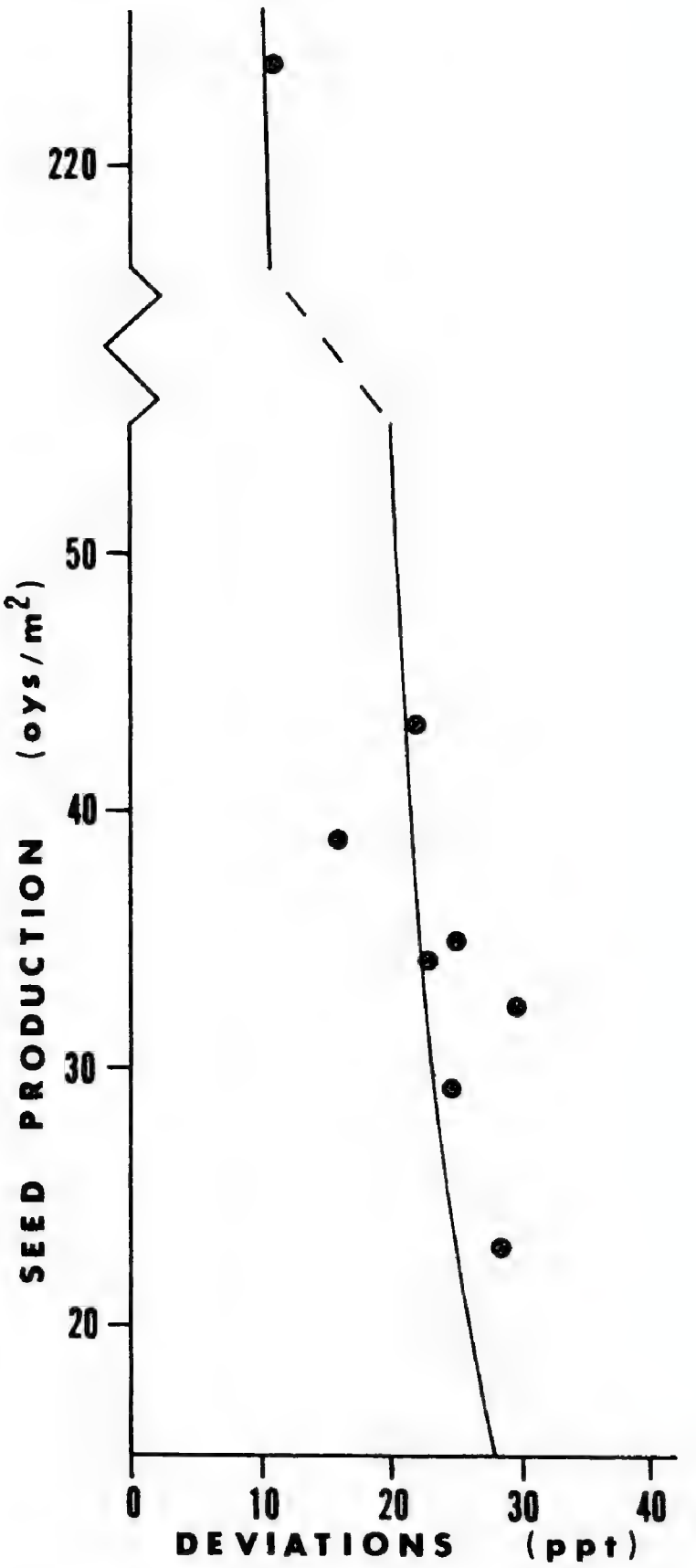

FIG. 7. Observed and predicted seed production, for those year/stations with good production, as a function of deviations from the optimum salinity regime.

When the 16 year/station regimes followed by poor seed production are incorporated into the plot of the 8 year/station regimes followed by good production, the same general relationship holds true (Fig. 8). Seed produc-

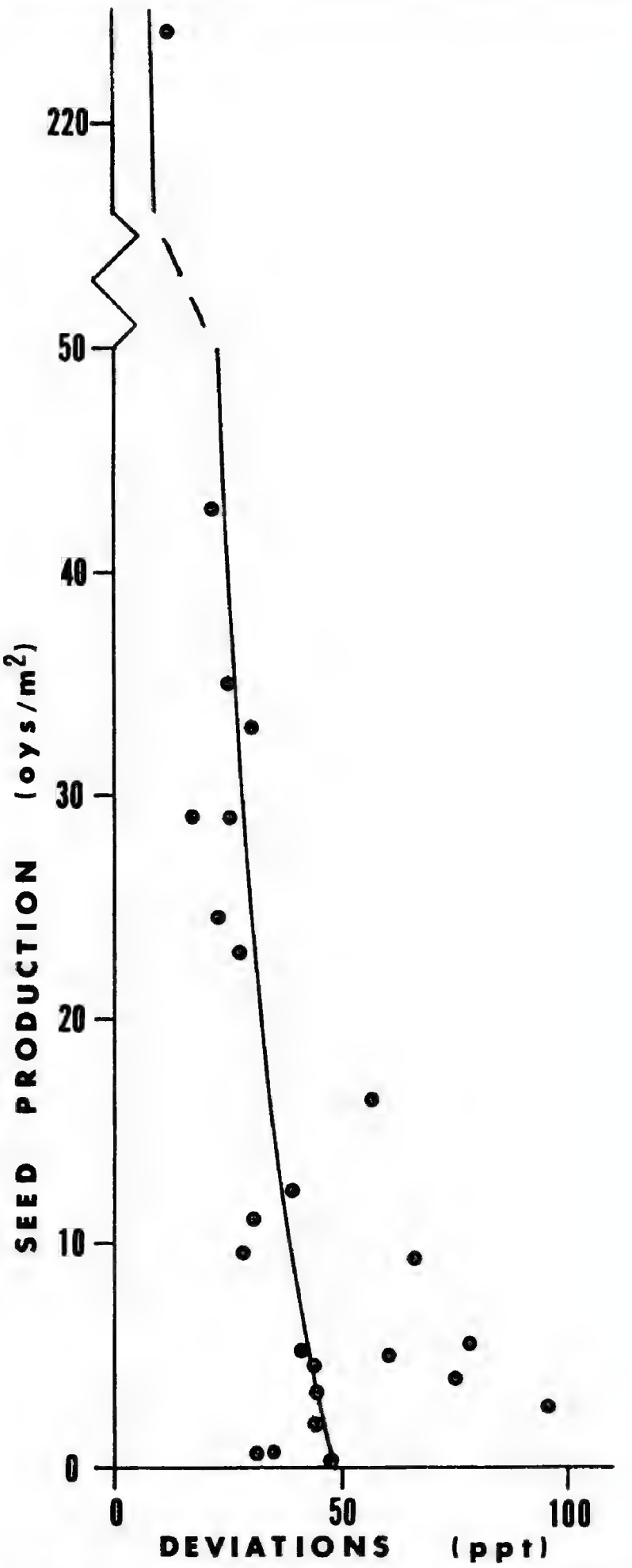

FIG. 8. Observed and predicted seed production for all year/stations as a function of deviations from the optimum salinity regime.

tion decreased as the sum of the monthly deviations from the composite regime increased. The equation expressing the relationship for all 24 year/station regimes is:

$$\text{Seed production} = -43.89 + 2144.5\ (\Sigma \text{ monthly deviations}^{-1})$$
$$\text{with } R^2 = 0.70;\ F = 51.3;\ p < 0.001;\ n = 24.$$

It appears from these two relationships that the composite drawn from the eight year/station regimes followed by good seed production is a sound estimate of the optimum salinity regime for the production of seed oysters. Hereafter, it will be referred to as the optimum regime.

Of the 16 year/station regimes followed by poor seed production, 13 deviated from the optimum primarily due to high salinities and 3 due to low salinities. Figure 9 shows a composite of the 13 high salinity regimes, the

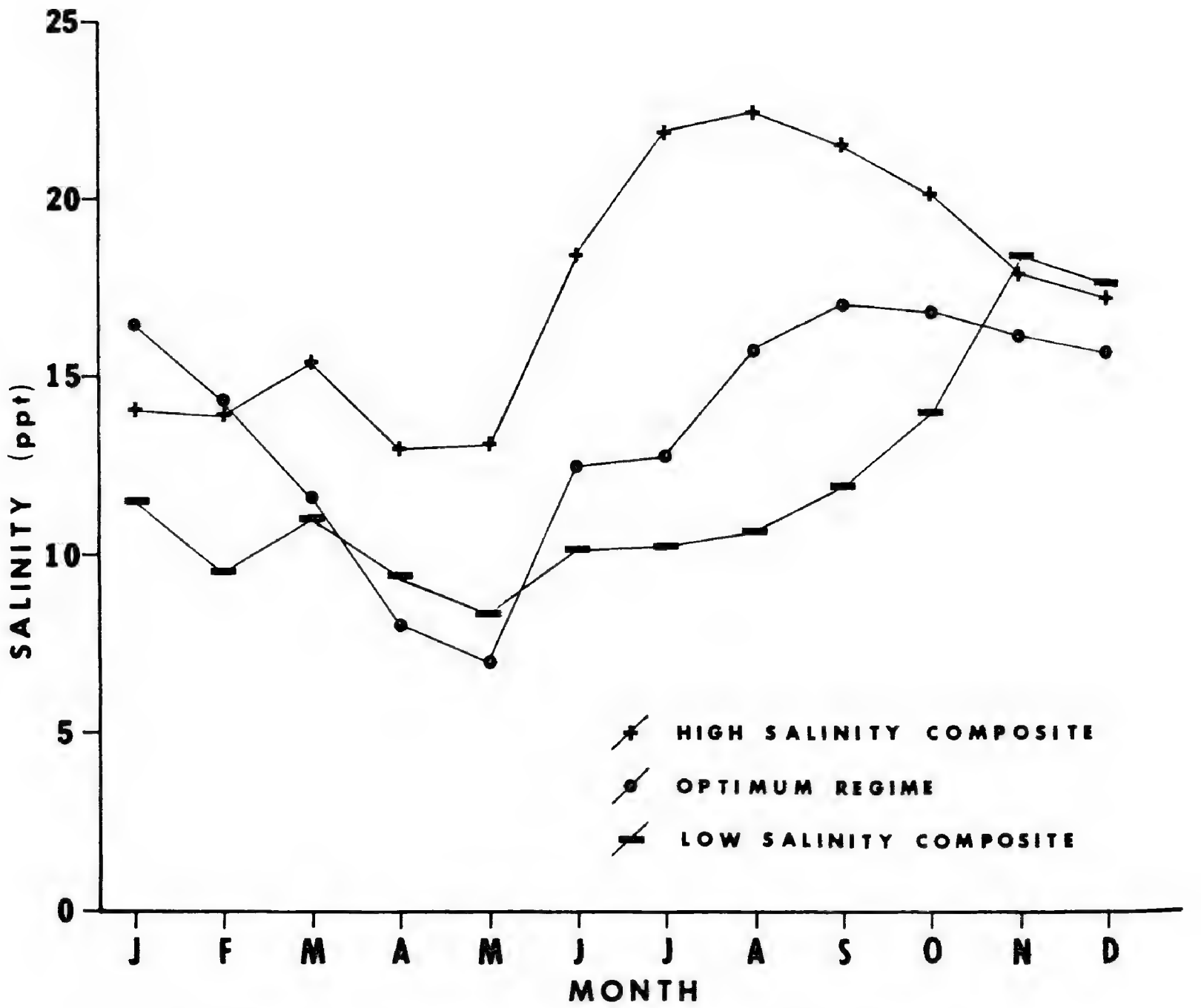

FIG. 9. Comparison of high salinity composite, optimum salinity regime, and low salinity composite.

optimum salinity regime, and a composite of the 3 low salinity regimes. Differences between the optimum regime and the high and low salinity composites are most pronounced for May through September, which indicates that summer salinities may be particularly important in the production of seed oysters. This is further supported by Ulanowicz, Caplins and Dunnington (1980) in their use of spawning season salinities for the prediction of spat densities, and by Gunter (1955) who found that salinity conditions during the summer months determine the extent of predator induced mortalities.

CONCLUSIONS

Salinity in the setting year is perhaps the prime determining factor for the production of seed oysters on the Louisiana state seed grounds. Both high and low extreme salinities are associated with poor seed production. While poor production at the low salinities can be related to insufficient setting, the mechanisms by which high salinities limit production are speculative in the absence of more specific mortality data. We believe, however, that high salinities allow for the proliferation of numerous organisms which adversely affect setting and recently set oysters. The largest differences between the optimum regime and the high salinity regimes were seen in May through September, the time in which virtually all setting occurs.

Since the optimum salinity regime was based on recorded successes in seed production, the regime is sensitive to the direct and indirect relationships between salinity and seed production. In effect, the regime represents the salinity profile for maximum observed seed production. Knowledge of the relationship of salinity to production has several possible applications. Success or failure of seed production in a given year could be predicted by the overall regression equation that relates seed production to deviations from the optimum regime. Also, cultch planting operations could be planned to take full advantage of favorable salinities. Perhaps the greatest potential application for the optimum regime, however, lies in managing the proposed freshwater diversions for maximum seed oyster production. The timing and magnitude of the diversions should be controlled to establish the optimum regime over those areas of maximum reef density on the seed grounds.

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STOMACH CONTENTS OF SELECTED FISHES FROM TEXAS BAYS

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ABSTRACT

The stomachs of 1245 fish representing 17 species were examined during November 1975–July 1976. The fish, 64.7% of which were collected with an 18.3-m bag seine, ranged in size from 14 to 305 mm standard length. The number of fish collected per bay system ranged from 91 in the Galveston Bay system to 216 in the San Antonio Bay system. The number of species collected per bay system ranged from 11 in the San Antonio Bay system to 15 in the lower Laguna Madre system. The number of stomachs analyzed per species ranged from 5 *Brevoortia patronus* to 199 *Micropogonias undulatus.*

The stomachs of *B. patronus* and *Mugil cephalus* contained plants only. Stomachs of the remaining species except *Paralichthys lethostigma* contained arthropods and miscellaneous items primarily. Fish were found in 60% of the *P. lethostigma* stomachs. Small and juvenile estuarine fish provide the link through which plants, micro-crustaceans and fish are transported to large predators. Although these were the primary items consumed, small fish also consume protozoans, rotifers, cnidarians, nemerteans, annelids and mollusks, which indicates their ability to consume and utilize many types of food.

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INTRODUCTION

Increasing demands are being placed on estuarine areas in the northwestern Gulf of Mexico to provide sites for residential and industrial development, recreational opportunities and food supplies. To meet these demands and maintain the valuable resources of the estuaries, it is essential that reliable population models, which contain identifiable food chains as their basis, be developed. Information on the food habits of fish along the Texas coast is limited; most of the existing reports deal only with commercially important species (Pearson 1929, Gunter 1945, Miles 1949, Guest and Gunter 1958, Simmons and Breuer 1962, Colura, Hysmith and Stevens 1976). Information on the food of juvenile or small fish (< 200 mm) is even more limited. Diener, Inglis and Adams (1974) identified the stomach contents of 40 fishes (12–610 mm) from Clear Lake, Texas, and concluded that the two primary food chains described by Darnell (1958) for Lake Pontchartrain, Louisiana, were not readily apparent for Clear Lake.

The objective of this study was to identify the stomach contents of selected juvenile fishes from Texas bay systems. A comparison of the relative importance of each class of food among the fishes examined is made. The study can also be used to determine the extent to which identified organisms serve as food for the fish examined.

AREA DESCRIPTION

The Texas coast is about 590 km long and contains eight major bay systems that cover an area of about 543,914 ha (Fig. 1). The size of individual bay systems ranges from the 6,475 ha of Sabine Lake to the 35,743 ha of Galveston Bay (Diener 1975). Most of the Texas coast is bordered by a chain of narrow barrier sand islands. Seawater from the Gulf of Mexico intrudes into the bay systems through passes between the islands. Much of the water movement in the bays is a result of wind action. Tidal amplitudes are generally < 0.6 m. Salinity ranges from 0 ‰ near river mouths to > 40 ‰ in Laguna Madre. The bay systems are shallow; the depth in unmodified areas usually does not exceed 3 m. Salt and brackish water marshes surround the bay systems. Submerged vegetation is often plentiful, especially in the more southern coastal areas.

MATERIALS AND METHODS

All eight Texas bay systems were sampled during November 1975–July 1976. Of the 1245 fish collected, 64.7% were taken with 18.3-m bag seines, 12.8% with 3-m trawls, 8.8% with cast nets, 7.8% with gill nets, 2.9% with 12.2-m bag seines, 1.0% with 7.6-m trawls, 1.0% with 4.6-m trawls and 1.0% with perch traps. Red drum *(Sciaenops ocellatus)* $\leq$ 305 mm standard length (SL) and other fish $<$ 203 mm SL were collected. All fish were immediately preserved in 10% formalin; the abdomens of large fish were first slit to allow better penetration of the fixative.

In the laboratory each fish was washed, identified and measured to the nearest mm SL. The stomach was then removed from the fish and opened. Food items from fish other than *Mugil cephalus* and *Brevoortia patronus* were identified to the lowest recognizable taxon and counted with the aid of a dissecting microscope.

The contents of the muscular pyloric region of the stomachs from each of *M. cephalus* and *B. patronus* were put into a 10-ml graduated centrifuge tube and water was added to make a known volume. This mixture was then stirred into suspension and a subsample was removed with a pipette. A portion of the subsample was put onto a hemacytometer. The food items on 10 squares (equivalent to 0.001 ml) were identified to the lowest recognizable taxon and counted. The following empirically-derived formula was used to calculate the density of each taxon in the total stomach contents:

$$D = \frac{V(C)}{0.001 \text{ ml}}$$

where: D = density of a single taxon in the total stomach contents
V = known volume of total stomach contents
C = number of individuals counted for a taxon in the 0.001-ml subsample

Percent frequency of occurrence was determined for each food item by dividing the number of fish containing the food item by the number of fish examined per species. Miscellaneous items found in the stomachs were defined as organic debris, organic matter, vascular plant debris and sand. Organic debris consisted of a heterogenous mixture of organic material; organic matter consisted of animal tissue digested beyond identification.

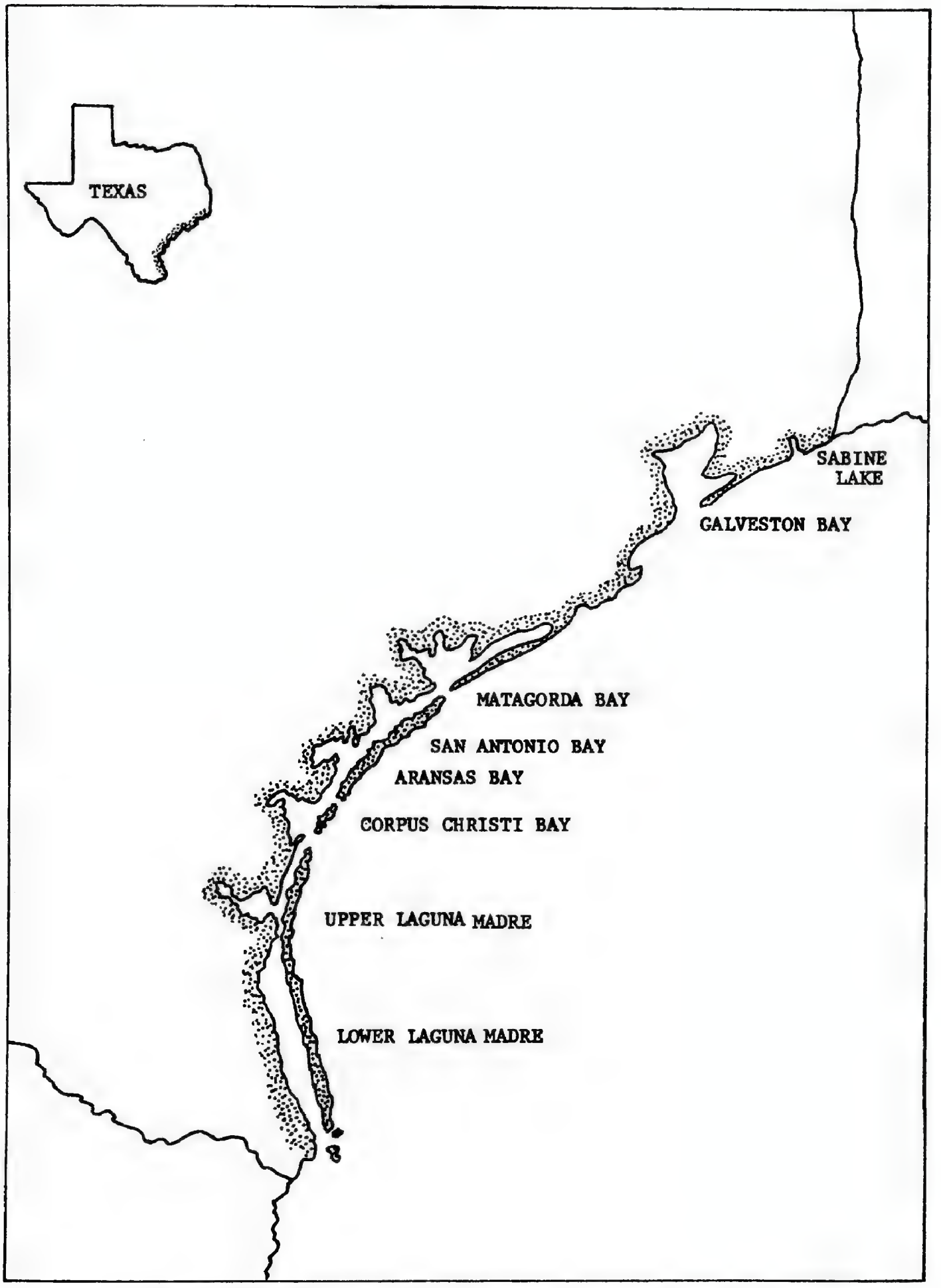

FIG. 1. Eight Texas bay systems where samples were collected.

RESULTS

Stomachs from 1245 fish representing 17 species were examined (Table 1). About 100–200 fish were collected in each bay system with at least 2 of the

TABLE 1

Number and size (standard length in mm) of fish examined by species and bay system.

Species	Size range	Sabine Lake	Galveston Bay	Matagorda Bay	San Antonio Bay	Aransas Bay	Corpus Christi Bay	Upper Laguna Madre	Lower Laguna Madre	Total	Stomachs with food (Number)
Sciaenops ocellatus	25-305	23	3	16	45	15	13	5	30	140	135
Cynoscion nebulosus	50-188	1	0	7	0	4	1	7	23	43	37
Archosargus probatocephalus	15-172	1	1	0	0	9	0	5	31	47	42
Pogonias cromis	26-225	1	7	10	18	2	3	0	11	52	50
Micropogonias undulatus	19-196	48	25	23	24	19	14	8	38	199	199
Anchoa mitchilli	28-72	9	7	5	0	7	5	14	4	52	47
Leiostomus xanthurus	18-192	19	19	29	24	19	14	12	27	163	159
Cynoscion arenarius	44-225	2	4	3	0	0	0	1	8	18	16
Paralichthys lethostigma	36-177	1	0	5	2	2	0	0	0	10	9
Menidia beryllina	18-85	5	1	15	15	5	21	0	0	62	54
Bairdiella chrysoura	55-112	0	0	0	0	0	0	1	5	6	6
Lagodon rhomboides	14-151	3	2	10	16	14	17	29	16	107	103
Cyprinodon variegatus	19-67	2	9	15	15	18	15	13	5	92	87
Fundulus similis	27-94	0	5	23	25	23	21	9	5	111	105
F. grandis	25-115	14	4	19	31	20	14	16	1	119	102
Mugil cephalus	29-196	0	1	0	0	14	1	1	2	19	16
Brevoortia patronus	57-183	0	3	0	1	0	0	0	1	5	5
Total		129	91	180	216	171	139	122	197	1245	1172

17 species caught in each bay system. Stomachs from at least 10 individuals of each species except *Bairdiella chrysoura* (6 fish) and *Brevoortia patronus* (5 fish) were examined. Of the 1245 stomachs examined, food was found in 1172.

The stomachs of *B. patronus* and *M. cephalus* contained plants only (Table 2). Bacillariophytes were the most common organisms encountered in *M. cephalus* (found in 84.2% of the fish examined) and *B. patronus* (found in 100.0% of the fish examined). Stomachs of the remaining species except

TABLE 2

Percent occurrence of food items in the stomachs of 19 *Mugil cephalus* (29–196 mm SL) and 5 *Brevoortia patronus* (57–183 mm SL). (Blanks = 0.0%).

Food organism or material recovered	*M. cephalus*	*B. patronus*	Food organism or material recovered	*M. cephalus*	*B. patronus*
BACILLARIOPHYTA			BACILLARIOPHYTA (Cont'd.)		
Achnanthes clevei		20.0	*Hemidiscus handmaniana*	10.5	
Achnanthes hauckiana	26.3	40.0	*Licmophora tincta*	21.1	
Achnanthes lemmermanni	5.3		*Mastogloia* sp.	5.3	
Achnanthes longipes	10.5		*Melosira moniliformis*	21.1	
Achnanthes spp.	47.4	60.0	*Navicula accomoda*	5.3	
Amphipleura pellucida	10.5		*Navicula arvensis*	15.8	20.0
Amphiprora protcoides	5.3		*Navicula halophila*	5.3	
Amphora marina	5.3		*Navicula latens*	5.3	
Amphora spp.	79.0		*Navicula obtusa*	15.8	
Amphora spectabilis	5.3		*Navicula pygmaea*	15.8	20.0
Amphora tennitrina	5.3		*Navicula radiosa*	5.3	
Asterionella bleakeleyi	10.5		*Navicula rhyncocephala*	15.8	
Asterionella japonica	5.3	40.0	*Navicula* sp.	47.4	20.0
Bacillaria paradoxa	10.5		*Neidium* sp.	5.3	
Biddulphia pulchella	5.3		*Nitzschia angularis*	15.8	
Centric diatom	31.6	80.0	*Nitzschia apiculata*	15.8	40.0
Chaetoceros compressus	5.3		*Nitzschia closterium*	47.4	20.0
Chaetoceros decipiens		20.0	*Nitzschia communis*	10.5	
Chaetoceros sp.	5.3		*Nitzschia compressa*	26.3	20.0
Climacosphenia moniligera	5.3		*Nitzschia constricta*	5.3	
Cocconeis disculoides	5.3		*Nitzschia longissima*	21.1	
Cocconeis disculus	5.3		*Nitzschia panduriformis*	5.3	
Cocconeis pediculus	15.8		*Nitzschia proxima*	10.5	
Cocconeis placentula	5.3		*Nitzschia pungens*		40.0
Cocconeis sp.	36.8		*Nitzschia rigaformis*	5.3	
Coscinodiscus centralis	5.3	20.0	*Nitzschia sigma*	26.3	
Coscinodiscus excentricus	5.3	40.0	*Nitzschia spathulata*	15.8	
Coscinodiscus granii	15.8	20.0	*Nitzschia* sp.	21.1	20.0
Coscinodiscus radiatus	15.8	40.0	*Opephora martyi*	21.1	
Coscinodiscus sp.	26.3	40.0	*Opephora swartzii*	10.5	
Cyclotella sp.	47.4	80.0	*Opephora* sp.	5.3	
Cymbella sp.	5.3		Pennata diatom	79.0	100.0
Diatoma sp.		20.0	*Pleurosigma angulatum*	10.5	
Diploneis bombus	26.3		*Pleurosigma salinaium*	10.5	
Diploneis crabro	5.3		*Pleurosigma* sp.	5.3	
Diploneis elliptica	21.1		*Skeletonema costatus*	15.8	80.0
Diploneis smithii	10.5		Spores	10.5	20.0
Diploneis sp.	10.5		*Stichosiphon* sp.	5.3	

TABLE 2 (Continued)

Food organism or material recovered	*M. cephalus*	*B. patronus*	Food organism or material recovered	*M. cephalus*	*B. patronus*
Fragilaria brevistriata	5.3		*Suriella gemma*	15.8	
Fragilaria construens	10.5		*Suriella* sp.	10.5	
Fragilaria crotonensis	10.5		*Synedra fasciculata*	15.8	
Fragilaria sp	5.3		*Synedra* sp.	52.6	60.0
Grammatophora sp.	5.3		*Synedra superba*	5.3	
Guanardia fluccida		20.0	*Tabellaris fenestrata*	15.8	
Gyrosigma attenuatur	5.3		*Thalassiosira rotula*	5.3	
Gyrosigma balticum	5.3		*Thalassiosira* spp.	21.1	60.0
Gyrosigma fasciola	5.3		*Thallasionema nitzschioides*	21.1	20.0
Gyrosigma marcum	5.3		*Thallasiothrix frauenfeldii*	10.5	
Gyrosigma sp.	10.5		*Thallasiothris* sp.	5.3	20.0
Gyrosigma spencerii	10.5		Total	84.2	100.0
CHLOROPHYTA			CYANOPHYTA		
Closteriopsis longissima	5.3		*Anabaena* sp.	5.3	20.0
Coccoid green	5.3	20.0	*Aphanocapsa elachista*	5.3	
Cosmarium sp.	5.3	20.0	*Chroococcus* sp.	10.5	
Crucigenia sp.		20.0	*Chroococcus turgidus*		20.0
Green-unidentified	5.3		*Dactylococcopsis salararum*		20.0
Kirchneriella sp.	5.3	40.0	*Dactylococcopsis* sp.	5.3	
Scenedesmus acumenatus	5.3	20.0	*Merismopedia elegans*	5.3	
Scenedesmus armatus	5.3		*Merismopedia* sp.	15.8	
Scenedesmus bejuja	5.3	20.0	*Nostoc* sp.	5.3	
Scenedesmus quadricauda		20.0	*Oscillatoria* sp.		20.0
Scenedesmus sp.	10.5		Total	36.8	60.0
Tetraedron minimum		20.0	EUGLENOPHYTA		
Westella botryoides		20.0	*Euglena* sp.	5.3	
Total	26.3	80.0	Total	5.3	
CHRYSOPHYTA			PYRROPHYTA		
Campylodiscus cribrosus	10.5		Dinoflagellate	5.3	20.0
Campylodiscus sp.	10.5		*Exuviaella compressa*	5.3	
Hymenomonas cartarae	5.3		*Gymnodinium* sp.	5.3	
Hymenomonas sp.	5.3		*Peridinium minutum*		20.0
Total	21.1		*Prorocentrum micans*	10.5	20.0
CRYPTOPHYTA			*Prorocentrum minimum*		20.0
Phytoflagellates		20.0	*Prorocentrum* sp.	5.3	
Total		20.0	Total	21.1	80.0
			MISCELLANEOUS		
			Detritus	84.2	100.0
			Sand and Silt	84.2	100.0
			Total	100.0	100.0

Paralichthys lethostigma contained arthropods and miscellaneous items primarily (Figs. 2–5). Polychaetes were the most common annelids found

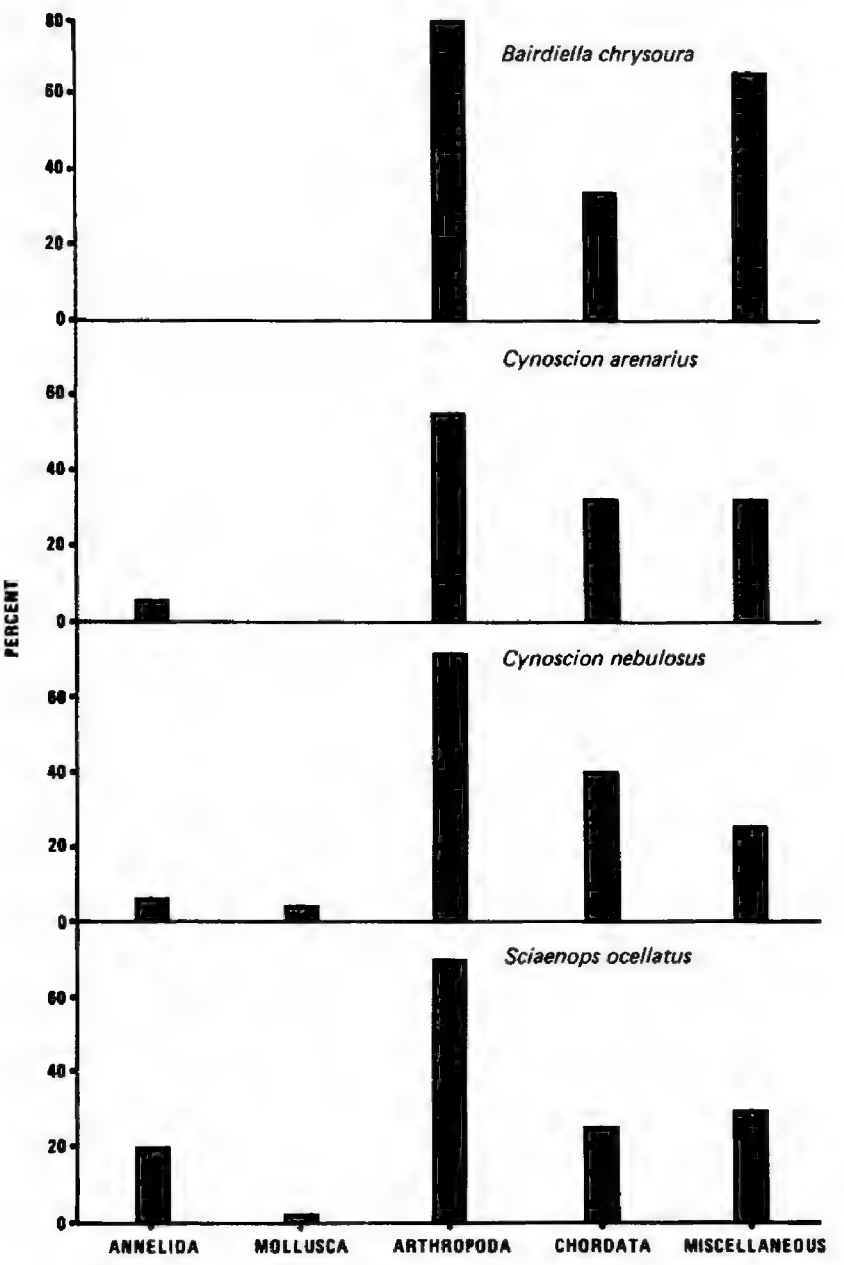

FIG. 2. Percent of stomachs of four fishes examined which contained representatives of each of five categories (numbers above X-axis indicate percent).

among species; bivalves were the primary mollusks encountered (Table 3). The arthropods most frequently found among fish species included gammarid copepods, mysids, shrimp, tanaids and *Corophium* species. Chordates, including *M. undulatus* and *Archosargus probatocephalus,* were found in 60% of the *P. lethostigma* stomachs (Fig. 3).

DISCUSSION

Juvenile predaceous fish in Lake Pontchartrain, Louisiana, provide the mechanism through which micro-crustaceans, clams, penaeid and palae-

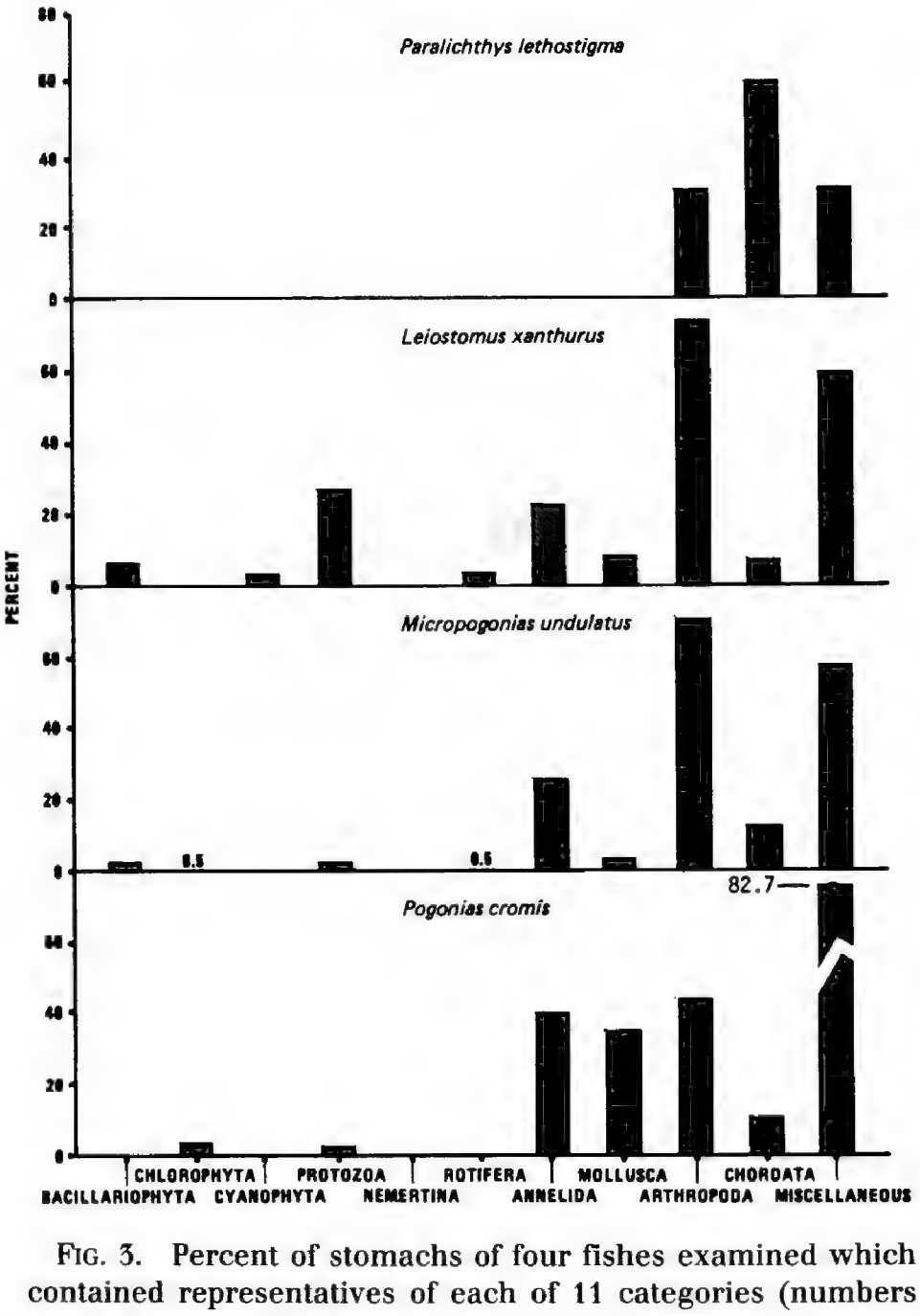

FIG. 3. Percent of stomachs of four fishes examined which contained representatives of each of 11 categories (numbers above X-axis indicate percent).

monid shrimp, and blue crabs are transferred through the food chain to large predators (Darnell 1958). This study indicates that juvenile and small fish in Texas bays may also transport these same organisms to large fish. However, fish in Texas apparently relied more heavily on arthropods than did fish in Louisiana. The apparent difference between fish in Texas and Louisiana may have been more a function of availability than preference.

Neither Texas nor Louisiana fish consumed only one group of organisms. Fish of each species from both areas ate animals that represent at least three different categories and thus can be considered omnivorous. Prey species of arthropods may have been more abundant in the Texas bay systems where fish were collected than in Louisiana. Darnell (1958) collected fish from along the shore and in open water whereas most of the fish collected during this study were caught along the shore. Weaver and Holloway (1974) indicated that organic detritus was a major component ingested by *B.*

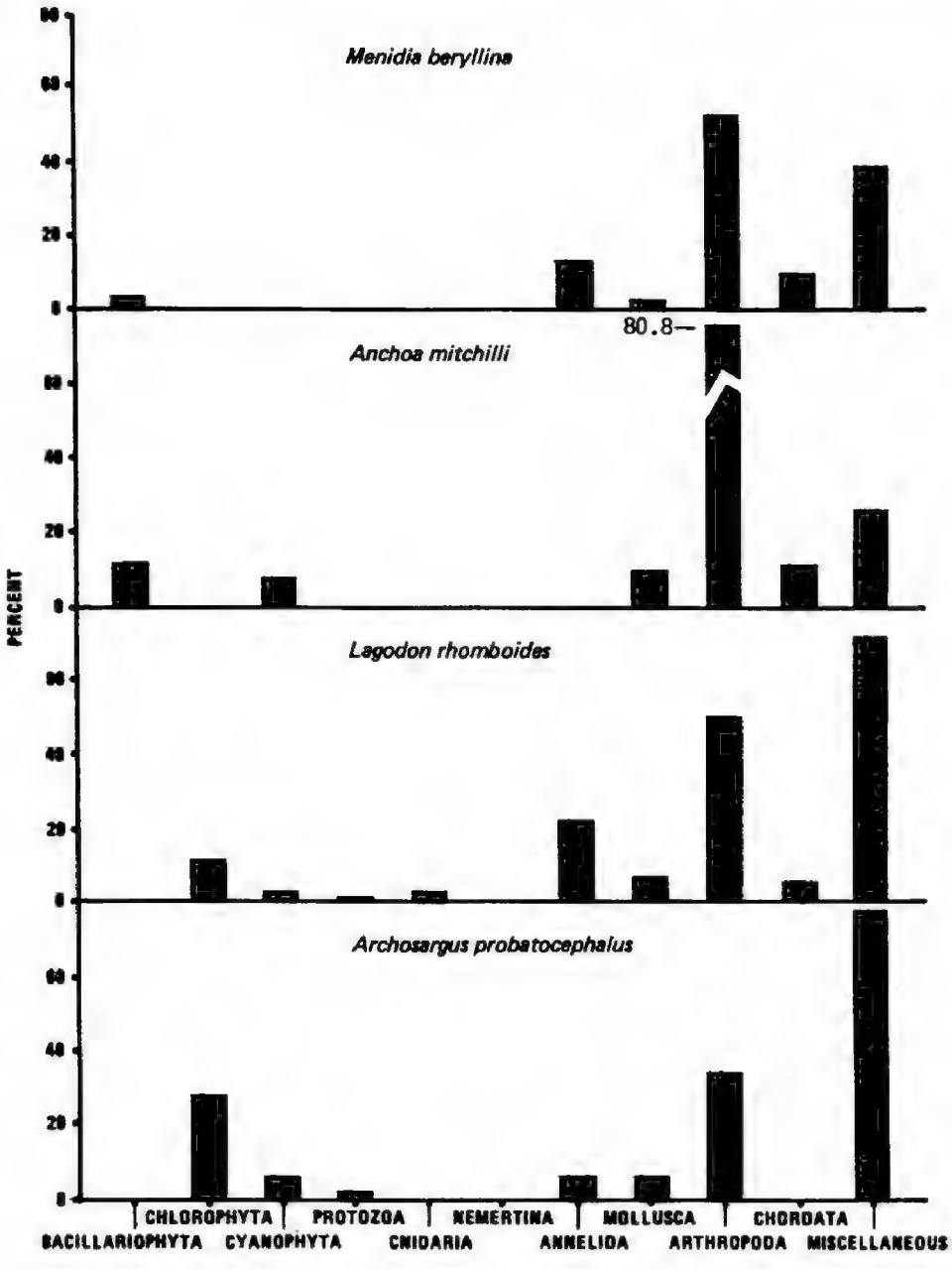

FIG. 4. Percent of stomachs of four fishes examined which contained representatives of each of 11 categories (numbers above X-axis indicate percent).

patronus, Anchoa mitchilli, Micropogonias undulatus and *Leiostomus xanthurus* in the open-water community while no organic detritus was found in *Lucania parva* or *Poecilia latipinna* in the vegetated community. Sheridan (1979) concluded that the diet of *M. undulatus* in shallow, low salinity areas of Apalachicola Bay ate mainly small crustaceans whereas fish in deep, high salinity areas ate mainly polychaetes.

The greater reliance on arthropods by Texas fish than by Louisiana fish may also have been related to the collection period. Fish in Louisiana were collected during June 1953–August 1954; Texas fish were collected during November 1975–July 1976. If the difference in food composition were due to the longer collection period in Louisiana than in Texas, a seasonal influence on food consumption may be indicated. Data presented by Moffett, McEachron and Key (1979) indicated that *Cynoscion arenarius* (45–159 mm SL) ate mainly fish in the spring and mainly penaeid shrimp in the fall. Sheridan (1979) identified temporal changes in the diets of *M. undulatus, L. xanth-*

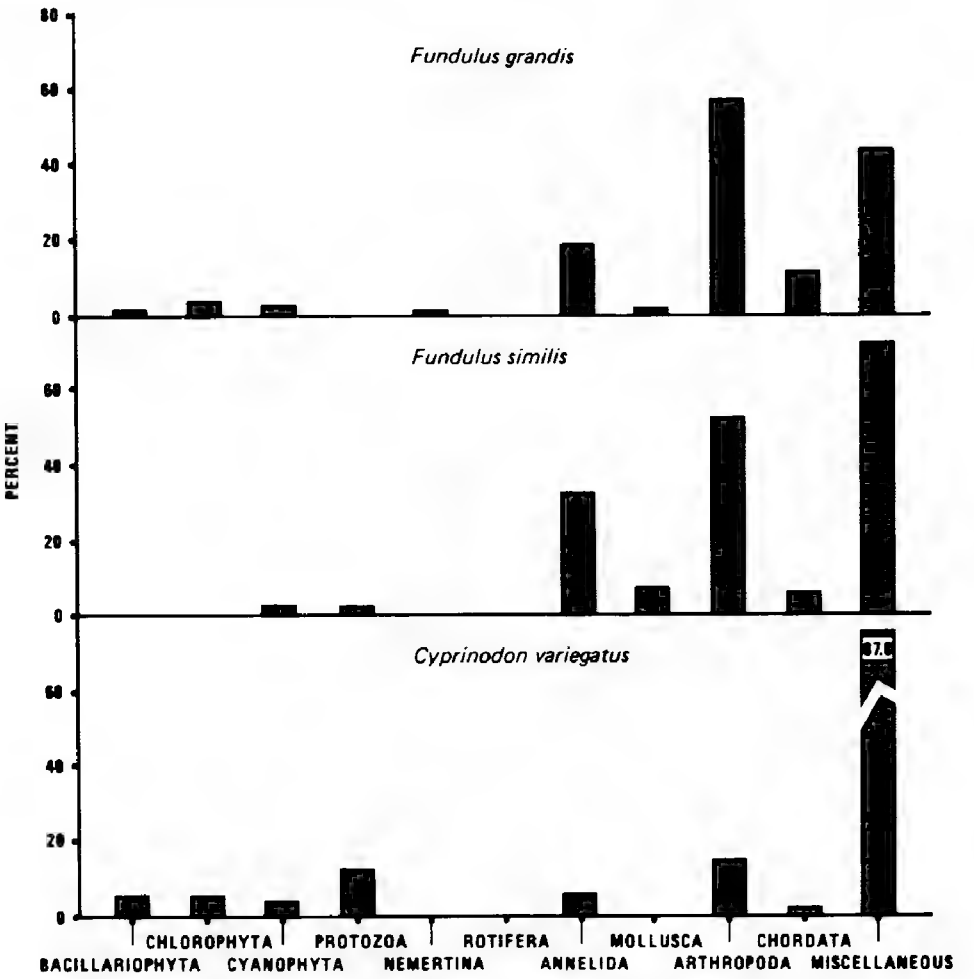

FIG. 5. Percent of stomachs of three fishes examined which contained representatives of each of 11 categories (numbers above X-axis indicate percent).

urus, and *C. arenarius* in Florida. Chao and Musick (1977) concluded that juvenile sciaenids are able to coexist in the same area because of differences in spatial and temporal distribution, relative abundance, and food habits. *Larimus fasciatus, C. regalis,* and *B. chrysoura* in Virginia fed mainly above the bottom on fishes and planktonic crustaceans; *M. undulatus, M. saxatilis,* and *L. xanthurus* fed on epifauna, infauna or both. In addition, partitioning of food among young sciaenids depends more on the habits of the prey species than on "selective preference" on the fishes.

Darnell (1958) found that large flounder (113–380 mm) were highly predaceous and consumed large quantities of small fishes, and he stated that young flounder probably prey upon small bottom invertebrates. In Texas, young flounder appear to consume the same type of food as larger flounder in Louisiana. Southern flounder (36–177 mm SL) examined during this study fed primarily on fish (including *A. probatocephalus* and *M. undulatus).* In North Carolina small southern flounder consumed fishes in the greatest quantity; mysids occurred most frequently but were not eaten in proportion to their abundance (Powell and Schwartz 1979). The preference of fishes by southern flounder in places where mysids were abundant may represent selective feeding (Powell and Schwartz 1979).

Harrington and Harrington (1961) reported that *Cyprinodon variegatus* generally fed on vegetation and noted that most stomachs contained sand.

TABLE 3

Contents of stomachs of 15 fishes from Texas bays (*Sciaenops ocellatus* = 1; *Cynoscion nebulosus* = 2; *Pogonias cromis* = 3; *Micropogonias undulatus* = 4; *Leiostomus xanthurus* = 5; *C. arenarius* = 6; *Bairdiella chrysoura* = 7; *Archosargus probatocephalus* = 8; *Lagodon rhomboides* = 9; *Paralichthys lethostigma* = 10; *Anchoa mitchilli* = 11; *Menidia beryllina* = 12; *Cyprinodon variegatus* = 13; *Fundulus similis* = 14; *grandis* = 15).

Food organism or material found	Sciaenidae							Sparidae		Bothidae	Engraulidae	Atherinidae	Cyprinodontidae		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
BACILLARIOPHYTA				X	X						X	X	X		X
Coscinodiscus sp.				X	X						X	X			
Diatoms					X						X		X		X
CYANOPHYTA					X			X	X		X		X	X	X
Blue-green algae					X			X	X		X		X	X	X
CHLOROPHYTA			X	X				X	X				X		X
Green algae			X	X				X	X				X		X
PROTOZOA			X	X	X			X	X				X	X	
Foraminiferan			X	X	X			X	X				X	X	
ROTIFER				X											
Brachionus plicatilis				X											
CNIDARIA									X						
Sea anemone									X						
NEMERTINA					X										X
Nemertean					X										X
ANNELIDA	X	X	X	X	X	X		X	X			X	X	X	X
Arenicola cristata				X											
Diopatra cuprea	X											X			
Nereis occidentalis															X
Nereis succinea	X			X	X				X						X
Nereid polychaete	X			X	X				X			X	X	X	X
Polychaete larvae					X				X						
Polychaete worm			X						X					X	
Polychaete remains	X	X	X	X	X	X		X	X			X		X	X
Serpulid worm								X							
Terebellid polychaete					X										
MOLLUSCA	X	X	X	X	X			X	X	X		X		X	X
Brachidontes exustus										X					
Congeria leucophaeta									X						
Crepidula plana															X
Laevicardium mortoni								X	X						
Macoma constricta										X					
Macoma mitchilli					X										

TABLE 3 (Continued)

Food organism or material found	Sciaenidae							Sparidae		Bothidae	Engraulidae	Atherinidae	Cyprinodontidae		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mitrella lunata	X														
Mulina lateralis				X											
Neritina reclivata				X											
Rangia cuneata			X		X										
Bivalve	X	X	X	X	X			X	X					X	
Bivalve veligers										X		X			
Gastropod			X	X										X	
Gastropod veligers			X							X		X		X	
ARTHROPODA	X	X	X	X	X	X	X	X	X	X	X	X		X	X
Acartia tonsa				X	X				X		X	X			
Alpheus sp.		X													X
Bowmaniella brasiliensis	X			X	X										
Caligus sp.				X		X					X	X			
Callinectes sapidus	X				X		X	X	X						X
Cassidinidea lunifrons							X		X						
Centropages hamatus											X				
Clibinarius vittatus															X
Corophium sp.	X		X	X	X			X	X		X	X		X	X
Edotea triloba												X			
Ergasilus sp.	X														
Euceramus sp.											X				
Eurypanopeus depressus								X	X						
Eurytemora hirumdoides				X	X			X	X			X			
Eurytemora sp.				X											
Gammarcus mucronatus	X		X	X	X				X						X
Hippolyte pleurocartha	X								X						
Labidocera aestiva				X	X				X			X			
Leptochelia sp.				X	X										X
Mysidopsis almyra	X	X		X	X	X	X		X		X				
Mysidopsis sp.	X	X		X				X	X						
Neopanope texana				X											
Ogyrides limicola				X		X			X						
Oithona sp.									X		X				
Palaemonetes intermedius	X														
Palemonetes pugio	X	X		X		X				X					X
Palaemonetes sp.	X	X		X					X		X	X		X	X
Penaeus aztecus	X	X													

TABLE 3 (Continued)

Food organism or material found	Sciaenidae							Sparidae		Bothidae	Engraulidae	Atherinidae	Cyprinodontidae		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
ARTHROPODA (Cont'd.)															
Penaeus setiferus				X											
Penaeus sp.	X			X	X	X									
Pinnotheres sp.												X			
Pseudodiaptomus coronatus				X	X				X		X				
Scottolana canadensis				X	X										
Taphromysis louisianae											X	X			
Tozeuma carolinense	X														
Arachnid												X			X
Barnacle									X						
Barnacle cyprids					X				X		X	X		X	
Barnacle nauplii					X				X		X		X		
Calanoid copepod					X			X	X		X	X	X		
Caprellid amphipod															X
Ceratopogonid midge					X										
Chironomid larvae				X											
Coleopteran									X						
Copepod	X			X					X		X			X	X
Crab	X		X	X				X	X						X
Crab zoea				X							X				
Curculionid - weevil														X	X
Cyclopoid copepod				X	X								X		
Dipteran fly			X	X								X		X	X
Dipteran pupa			X												
Dytiscid adult														X	
Ephemeropteran	X														
Formicid ant								X			X	X		X	X
Gammarid copepod	X	X	X	X	X	X	X	X	X		X	X	X	X	X
Harpacticoid copepod				X	X			X	X		X	X	X	X	X
Hydracarina														X	
Insect				X	X							X	X	X	X
Isopod	X				X				X					X	X
Mysid	X	X	X	X	X	X	X	X	X		X				
Odonation adult			X		X										
Ostracod				X	X						X	X	X	X	
Serpulid worms									X						
Shrimp	X	X	X	X	X		X		X	X	X	X		X	X
Shrimp zoea											X	X			X

TABLE 3 (Continued)

Food organism or material found	Sciaenidae							Sparidae		Bothidae	Engraulidae	Atherinidae	Cyprinodontidae		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
ARTHROPODA (Cont'd.)															
Tanaid	X	X	X	X	X			X	X		X		X	X	X
Tendipedidae larvae			X	X	X			X						X	X
Tendipedidae pupa				X											
Trichoptera larvae											X				
Xanthid crab	X		X												
CHORDATA	X	X	X	X	X	X	X		X	X	X	X	X	X	X
Anchoa mitchilli	X	X		X		X						X			
Brevoortia patronus	X	X			X										
Fundulus similis	X														
Leiostomus xanthurus	X														
Lucania parva	X														
Micropogonias undulatus	X									X					
Mugil cephalus	X														
Archosargus probatocephalus							X			X					
Fundulus grandis															X
Menidia beryllina		X													
Fish larvae			X						X						
Fish remains	X	X	X	X	X	X			X	X	X	X		X	X
Fish scales	X		X	X	X	X	X		X			X	X	X	X
Silverside		X													
MISCELLANEOUS	X	X	X	X	X	X		X	X	X	X	X	X	X	X
Fecal pellets			X	X	X				X			X	X	X	X
Organic debris	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Organic matter	X	X	X	X	X	X		X	X	X	X	X	X	X	X
Sand	X	X		X	X			X	X		X	X	X	X	X
Vascular plant debris	X	X		X	X		X	X	X				X	X	X

During this study sand and organic debris were also found frequently (87% of the stomachs examined); however, arthropods and protozoans were more often found than plants. Again, the apparent difference may have been due to availability. Harrington and Harrington (1961) also examined stomachs of *Fundulus grandis* and found primarily arthropods. Arthropods were also the major food organisms found in the stomachs of *F. grandis* during this study.

Both *M. cephalus* and *B. patronus* examined during this study fed primarily on diatoms, detritus, and sand and silt. Darnell (1958) reported that *M. cephalus* fed primarily on bottom surface material while *B. patronous* fed

primarily on planktonic algae and microcrustaceans. Diatoms were conspicuously absent from the fish examined by Darnell (1958). Perhaps the turbid nature of the environment from which the Louisiana fish originated prevented the identification of diatoms in the examined stomachs. The herbivorous diet of juvenile *M. cephalus* and *B. patronus* in Texas indicates that a food chain not identified by Darnell (1958) may exist: namely, from diatoms and phytoplankton to small fish to large predators.

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ANALYSIS OF SPATIAL AND TEMPORAL VARIATIONS IN BIOMASS AND COMMUNITY STRUCTURE OF MOTILE ORGANISMS IN TOWN CREEK, A SOUTH CAROLINA TIDAL PASS[1]

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ABSTRACT

Spatial and temporal variations in six variables—number of species, number of individuals, total biomass, biomass concentration, H'_n species diversity, and H'_w biomass diversity—were investigated for nektonic and macroplanktonic organisms across a transect in the Town Creek estuary, South Carolina. Significant variation in most variables in the macrozooplankton was attributable to station, light, and tidal stage effects. Biomass concentrations, however, did not vary, an indication that biological constituents were well-mixed in the cross-section. Nekton concentrations varied significantly across the transect, as well as with time, light, and tidal stage; however, no one station was statistically different from all others. Invertebrates dominated both sets of collections in November. The opossum shrimp, *Neomysis americanus,* was the most common member of the macrozooplankton community and the bay anchovy, *Anchoa mitchilli,* was the most common nektonic organism; however, the blue crab, *Callinectes sapidus,* surpassed the anchovy in weight. *Anchoa mitchilli* ranked second numerically to *Brevoortia tyrannus* in April. Both fishes ranked third and second respectively by weight to the coelenterate *Cyanea capillata.* The results from these analyses were used in the design of a subsequent sampling program to assess the flux of materials through the transect over longer periods of time.

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INTRODUCTION

It is commonly assumed that most nektonic and planktonic organisms are neither randomly distributed nor regularly distributed throughout their available environment. Instead, these organisms may be clustered in

patches around localized food resources or other suitable microclimatological features, or clumped together due to other causative factors in their physical or biological histories. Most organisms which are capable of even limited movement also exhibit, in addition to spatial variations, variations over time which reflect patterns of biological activity and responses to temporally varying environmental factors. It is only when locomotory abilities of the organisms are literally overwhelmed by the physical environment that this patchiness disappears and distributions become more uniform.

Knowledge of such spatial and temporal variations in the distribution of organisms is vital for the design of sampling programs. Recent studies have examined such variations in the catch of zooplankton (Lee and McAlice 1979) and ichthyoplankton (Conte, Otto and Miller 1979), as well as larger trawl-caught organisms (Livingston 1976). These studies have determined ecological relationships between species and their environment and have elucidated variation and its sources in biological collections. The purpose of the present study was the investigation of spatial and temporal variations in the distribution and composition of macrozooplankton and nekton in Town Creek, Georgetown County, South Carolina (Figure 1), a coastal salt marsh inlet, in order to design a sampling program which could quantitatively assess the movement of these organisms in and out of the creek. This study was part of a larger multidisciplinary effort to determine the flux of materials through North Inlet. Kjerfve and Proehl (1979) and Chrzanowski, Stevenson and Kjerfve (1979) have previously reported results on the transport of water and microbial biomass through the Town Creek transect.

MATERIALS AND METHODS

STUDY AREA

North Inlet is a well-mixed, tidally driven, high-salinity, shallow arm of the Atlantic Ocean that consists of a series of tidal creeks draining a 30-km^2 salt marsh vegetated primarily with *Spartina alterniflora* (Figure 1). Town Creek, the largest, drains approximately 60% of the marsh and thus was expected to play a dominant role in the movement of organisms and other materials in and out of North Inlet. Factors which affect variations in the concentrations or composition of such materials in Town Creek should have major effects on the overall flux of the same materials between North Inlet and the Atlantic Ocean.

SAMPLING ROUTINE

On 12–18 November 1977, 10 boats (12–15′ open skiffs) were four-point moored across a 320-m transect established near the mouth of Town Creek (see Figures 1 and 2). Boats at stations A01 A08, andA10 served as sampling stations for macrozooplankton, as well as for samples of other materials *(i.e.,* phytoplankton, holozooplankton, dissolved nutrients, detritus). Physical data were recorded at all stations. In addition, a permanent platform located near station A01 served as a sampling station for nekton on 10–13 November 1977. Originally it was intended to sample both nekton and ichthyoplankton at several stations across the transect synoptically with other measurements; however, mechanical difficulties with the boat and motor prevented the cross-channel nekton collections at stations A05 and A08 from being made in November. These collections were finally undertaken on 7–8 April 1978. Comparable nekton collections

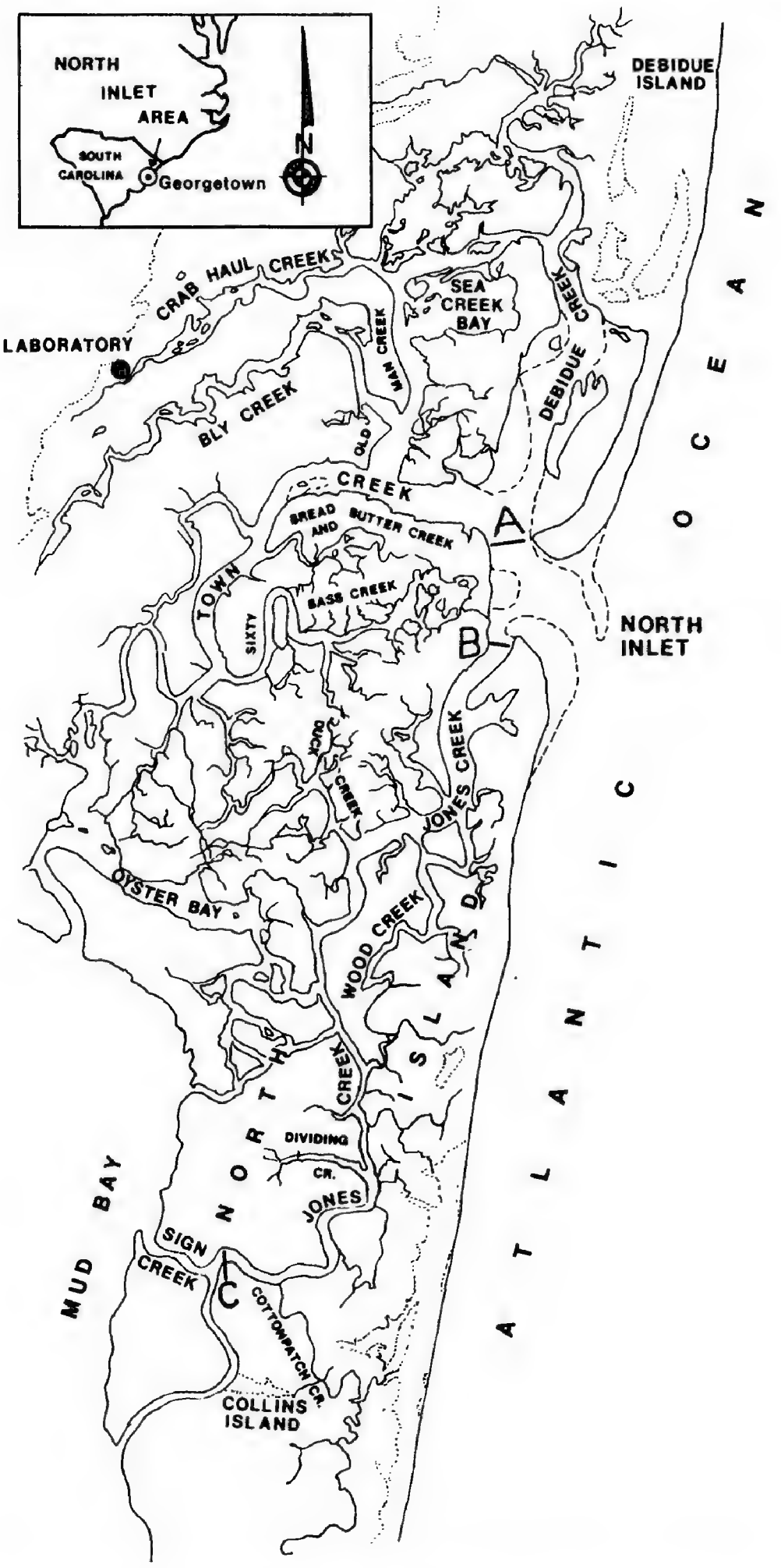

FIG. 1. Map of North Inlet Estuary showing location of sample transect (A).

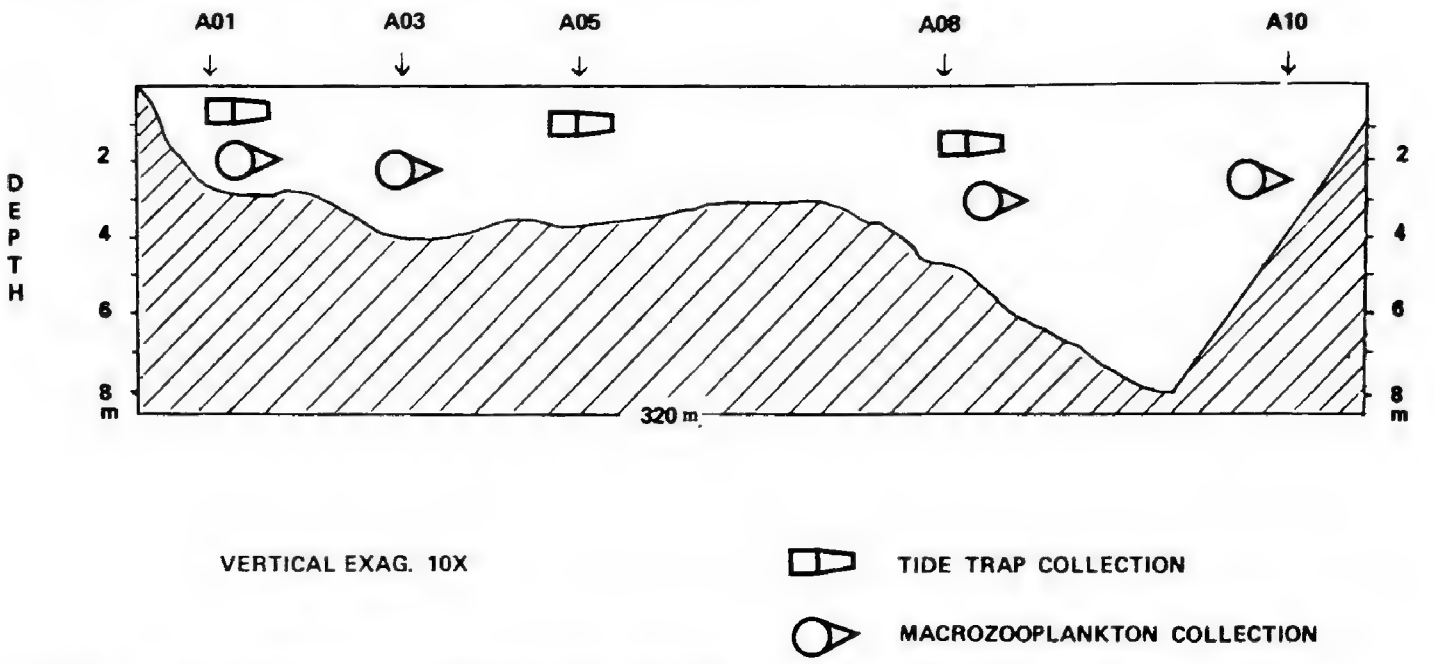

FIG. 2. Cross-section of experimental transect showing locations of nekton and macrozooplankton sampling stations.

made at station A01 during both sampling periods yielded similar patterns of catch statistics; thus the postponed collections did not affect our interpretation of the patterns of short-term variability in biomass concentration.

SAMPLING APPARATUS

Macrozooplankton samples were collected by means of 0.5-m-diameter nets constructed of 505-μ nitex material. A flowmeter in the mouth of each net determined the volume of water which passed through the net. The weighted nets were quickly lowered to the bottom and then raised, providing a depth-integrated sample of 5-min duration.

Nekton samples were taken using paired tide-traps modified from those used by Copeland (1965) and Birkhead (1977). These nets had an opening 1x2 m, were 5 m in length, and were constructed from 13-mm square mesh netting with a 6.5-mm square mesh bag sewn onto the cod end. One pair of nets was lowered on a frame between two pipes attached to the platform near station A01, while another pair of nets was deployed from either side of an outboard-powered boat which alternately made collections at stations A05 and A08.

Other investigators have made use of the "towing power" of tidal currents to capture larval fishes and macrocrustaceans in tidal inlets (Massman 1952; Dovel 1964; Lewis and Mann 1971; King 1971; Graham 1972; Duronslet, Lyon and Marullo 1972; Weinstein, Weiss, Hodson and Gerry 1980). Graham and Venno (1968) discussed problems associated with stationary nets, chiefly the effects of current velocity on catch efficiency. Our data indicated that at velocities of less than .25 m sec^{-1}, the nekton catch was significantly reduced and so collections at these low velocities were excluded from further analysis.

Macrozooplankton samples were of 5-min duration and nekton samples of 15-min duration. Samples were preserved in 4% formaldehyde and returned to the laboratory for enumeration. Data analysis utilized Statistical Analysis System (SAS) procedures available through the University of South Carolina's Computer Services. Since most of our questions were concerned with variations in our data, the ANOVA procedures and other options found in the SAS General Linear Models (GLM) procedure were used most commonly.

DATA ANALYSIS

Comparison of numerical and biomass data through ANOVA is a standard statistical procedure. Wohlschlag, Cole, Dobbs, Vetter and Moore (1976) used this method to demonstrate spatial and temporal changes in the demersal fish communities on the South Texas outer

continental shelf, while Moll and Rohlf (1981) used a similar analysis in their study of phytoplankton variability in Flax Pond, Long Island. In all our analyses, the following were treated as dependent variables: the number of species per tow *(S),* total number of organisms per tow *(N),* total biomass (g per tow, *BIOM),* biomass concentration ($g \cdot m^{-3}$,*BIOC),* and the two diversity indices H'_n and H'_w.

Variation in the dependent variables was investigated with respect to date, time, station, and, for nekton collections, replicate variation. Macrozooplankton samples were not replicated. Light (day or night), tide (ebb or flood), and eight tidal stages were considered (1. slack high, 2. early ebb, 3. mid ebb, 4. late ebb, 5. slack low, 6. early flood, 7. mid flood, and 8. late flood). Each stage of the tide lasted approximately 93 mins and represented the sampling interval for synoptic hydrographic measurements.

Initially, Bartlett's Test for homogeneity was used to test the distribution of variances of the numerical variables. These results indicated that the variances were not distributed homoscedastically. In such cases, logarithmic transformation of the data was in order (Sokal and Rohlf 1969). Consequently, *BIOM* and *BIOC* were logarithmically transformed, while the *S* and *N* underwent a square root transformation. In both cases, 1 was added to each raw value before transformation to eliminate values of zero. Initially, interaction as well as main effect terms were included in each analysis (Sokal and Rohlf 1969). The interaction terms were in all cases not significant ($p > 0.05$) and were deleted from the analyses reported in this paper.

RESULTS

MACROZOOPLANKTON

Station, light, and tidal stage were assessed as sources of variation in *S, N, BIOM, BIOC,* H'_n, and H'_w. The results of the ANOVA are summarized in Table 1 which shows the mean square and probabilities associated with the *F*-statistic from each comparison of dependent and independent variables. Significant variation ($p < 0.05$) in *S,* H'_n, and H'_w was attributable to station and light, while *BIOM* and H'_n varied significantly with respect to the tidal stage. No significant variation was observed in *BIOC,* which indicated more or less constant concentrations of fish larvae and macrozooplankton across the transect, as well as throughout the collection period. Although significant differences in several variables were attributed to station, in no case did one station differ significantly from the other three. One or two stations differed from one or two others; however, there were always intermediate stations which were significantly related (Table 2).

NEKTON—CROSS-CHANNEL VARIATION

The data from 7–8 April 1978 were analyzed using station, replicate, light, and tidal direction as independent variables (Table 3). Significant variation in all dependent variables was attributable in nekton collections to station, and indicated that catch parameters varied significantly across the transect (Table 4). Significant levels of variation in these parameters were also attributable to tide direction and light. Replicate samples did not differ significantly (except for *N),* indicating that the catches from the paired nets were comparable.

TABLE 1

Summary of ANOVA November 1977 Macrozooplankton Data. Values in the table are Mean Squares for each combination of variables and the error associated with each dependent variable. Dependent variables are: S = square root of the number of species, N = square root of the number of individuals, *BIOM* = $\log_{10}$ of the total biomass, *BIOC* = $\log_{10}$ of the concentration gms net weight/m^3, H'_n = Shannon-Weaver diversity index, and H'_w = weight diversity index. *df* = degrees of freedom associated with each independent variable. Probability levels are indicated by asterisks: * = $0.01<p<0.05$, ** = $0.001<p<0.01$, *** = $p<0.001$, no asterisks indicate $p>0.05$.

		INDEPENDENT VARIABLES			
		STATION	LIGHT	TIDAL STAGE	ERROR
	df	3	1	7	38
DEPENDENT VARIABLES:	*S*	1.6820*	3.9064**	0.9476	0.4408
	N	5.1978	30.8440	12.2035	13.0224
	BIOM	0.0470	0.0363	0.1637*	0.0498
	BIOC	0.0035	0.0015	0.0030	0.0046
	H'_n	2.2793**	2.0169*	0.8561*	0.3126
	H'_w	1.0510*	1.6269*	0.5872	0.3280

TABLE 2

Results of Duncan's Multiple Range Test performed on macrozooplankton data from November 1977. Mean values connected by underlines do not differ significantly.

	STATION			
VARIABLE	A01	A03	A08	A10
S	2.5846	2.1602	1.9626	1.7031
N	4.2102	3.3180	4.1131	4.6232
BIOM	0.1139	0.0974	0.0423	0.1788
BIOC	0.0124	0.0437	0.0066	0.0247
H'_n	1.3372	0.9354	0.3731	0.5252
H'_w	1.0987	0.7165	0.4554	0.4621

TABLE 3

Summary of ANOVA April 1978 Cross-Channel Nekton Data. Values in the table are mean squares for each combination of variables and the error associated with each dependent variable. Dependent variables and probability levels as in Table 1.

		INDEPENDENT VARIABLES				
		STATION	REPLICATE	LIGHT	TIDAL DIRECTION	ERROR
	df	2	1	1	1	
DEPENDENT VARIABLES:	*S*	2.5378***	0.0874	8.7601***	2.6332***	0.2113
	N	50.4337***	27.3831*	100.1597***	59.1721**	6.0679
	BIOM	1.9314*	0.4451	5.3684**	1.3429	0.5624
	BIOC	0.0045**	0.0006	6.4928***	1.3337*	0.0009
	H'_n	1.2144**	0.0006	6.4928***	1.3337*	0.1934
	H'_w	0.8960**	0.3237	5.1534***	2.0232***	0.1329

TABLE 4

Results of Duncan's Multiple Range Test performed on nekton data from April 1978. Mean values connected by underlines do not differ significantly.

	STATION		
VARIABLE	A01	A05	A08
S	2.3646	1.8198	1.7158
N	5.4782	2.7780	2.8061
BIOM	1.6004	1.0279	1.1562
BIOC	0.0358	0.0070	0.0179
H'_n	0.9739	0.6716	0.5021
H'_w	0.8423	0.5249	0.4594

NEKTON—24-HOUR VARIATION

Data collected between 0600 on 12 November 1977 and 0700 on 13 November 1977, were analyzed by ANOVA using replicate, light, and tidal stage as independent variables (Table 5). Tidal stage accounted for signifi-

TABLE 5

Summary of ANOVA November 1977 24-Hour Nekton Data. Values in the table are mean squares for each combination of variables and the error associated with each dependent variable. Dependent variables and probability levels as in Table 1.

		INDEPENDENT VARIABLES			
		REPLICATE	LIGHT	TIDAL STAGE	ERROR
	df	1	1	7	32
DEPENDENT VARIABLES:	*S*	0.1540	0.5435*	3.5829***	0.5041
	N	3.8281	2.6110	29.3655**	6.3105
	BIOM	0.1863	0.5949	3.4886**	0.8594
	BIOC	0.0035	0.0001	0.0032	0.0023
	H'_n	0.2003	0.3869	2.2747***	0.3663
	H'_ω	0.0333	0.2799	2.1884***	0.2337

cant variation in most dependent variables. Light and replicate did not contribute significantly to the observed variation in any dependent variable.

NEKTON—DAY-TO-DAY VARIATIONS

Data collected at approximately 0500, 1100, 1700, and 2300, between 2300, 10 November 1977 and 0500, 13 November 1977, were analyzed by ANOVA using replicate, date, time, tidal stage, and light as independent variables (Table 6.) Significant variation in all dependent variables occurred with respect to date, time, light, and tidal stage. As in other comparisons, the results did not vary significantly with respect to replicate (four samples from two sequential paired-net collections).

SPECIES COMPOSITION

Numerical and weight data are repeated for dominant macrozooplankton and nekton species in Table 7. The Atlantic croaker, *Micropogonias un-*

TABLE 6

Summary of ANOVA November 1977 24-Hour Nekton Data. Values in the table are mean squares for each combination of variables and the error associated with each dependent variable. Dependent variables and probability levels as in Table 1.

		INDEPENDENT VARIABLES					
		DATE	TIME	REPLICATE	LIGHT	TIDAL STAGE	ERROR
	df	3	3	1	1	7	26
DEPENDENT VARIABLES:	*S*	6.1994***	7.2791***	0.0113	0.3011***	2.1237***	0.4522
	N	89.1709***	78.1508***	0.1175	0.9173***	18.8375***	7.3016
	BIOM	3.2211**	4.5804**	0.4841	2.7897***	1.9582**	0.6682
	BIOC	0.0091***	0.0128***	0.0023	0.0069***	0.0032*	0.0016
	H'_n	1.8546**	2.8835***	0.0071	0.4111***	1.0227**	0.2984
	H'_w	3.4462***	4.2844***	0.1221	0.2694***	0.8926***	0.2072

TABLE 7

Predominant Organisms (ranked among the top ten by number or weight) Captured in Town Creek 10–13 November 1977 and 7–8 April 1978.

MACROZOOPLANKTON

SPECIES	OCCURRENCE*	NUMBER	WEIGHT (GRAM)
Acetes americanus	November	64	0.78
grammaridean amphipods	November	46	0.12
Lucifer faxoni	November	38	0.06
Membras martinica	November	4	9.33
Micropogonias undulatus	November	26	0.25
Neomysis americanus	November	1078	2.04
Ogyrides limicola	November	6	0.26
Palaemonetes pugio	November	19	1.04
Palaemonetes vulgaris	November	10	0.66
penaeid shrimp larvae	November	14	0.04
Portunus spinimanus	November	1	31.00
portunid crab larvae	November	49	0.27
Symphurus plagiusa	November	1	0.17
Synguathus louisianae	November	5	1.07
unidentified fish larvae	November	15	0.25

* No macrozooplankton collections were made in April.

NEKTON

SPECIES	OCCURRENCE	NUMBER	WEIGHT (GRAM)
Anchoa hepsetus	April	2	32
Anchoa mitchelli	November	909	1030
	April	509	718
Bairdiella chrysoura	November	22	620
Brevoortia tyrannus	April	864	949
Callinectes sapidus	November	199	3342
	April	31	572
Cyanea capillata	April	274	4706
Lagodon rhomboides	November	14	602
Leiostomus xanthurus	April	117	271
Lolliguncula brevis	November	110	319
	April	179	472
Membras martinicas	November	24	52
	April	22	88
Menidia menidia	April	68	262
Mnemiopsis leidyi	April	--	216
Myrophis punctatus	November	33	691
Palaemonetes pugio	November	34	9
	April	15	2
Palaemonetes vulgaris	April	28	5
Penaeus duorarum	November	77	191
Penaeus setiferus	November	130	443
Portunus gibbesi	November	123	342
Portunus spinimanus	November	18	218
Prionotus tribulus	April	33	9
Stomolophus meleaguis	November	2	873
Trachypenaeus constrictus	November	279	56

dulatus, was the only fish species among the 10 most abundant macrozooplankton taxa. Fishes, however, contributed more biomass than did invertebrate plankters. Invertebrates dominated the nekton collections numerically in November, but the Atlantic menhaden *Brevoortia tyrannus* was the most commonly encountered species in April.

DISCUSSION

The goal of this study was to assess spatial and temporal variation in biomass concentration and to design a sampling schedule that would provide meaningful data within the constraints of time and budget. It was our plan ultimately to sample over a fortnightly period at four transects covering all major creek systems in North Inlet, and it was impossible to maintain both the number of stations at each transect and the sampling frequency attempted in our initial efforts during such an expanded sampling regime. To determine an optimum strategy, relative sampling efficiencies were calculated for various postulated sampling regimes using the method described by Sokal and Rohlf (1969). Since the flux of material (nekton, macrozooplankton, or other class) depends only on biomass concentration, only the data for this variable were analyzed. For macrozooplankton far more samples could be taken with available equipment and personnel than could be processed in the time available between proposed seasonal sampling periods; hence, we were interested in determining how to allocate the number of samples which could be processed. Since there were no significant differences in macrozooplankton biomass concentrations across the Town Creek transect, a reduction of stations was justified. Relative efficiencies were calculated for combinations of 1, 2, and 3 stations with the number of samples per station varying between 6 and 48 (Table 8). Between 24 and 32 collections would be needed at a single station to provide a sensitivity to fluctuations in biomass concentration equal to or greater than that provided by the trial effort. Since 48 samples per transect were estimated to be the maximum which could be processed, it would be possible to sample at a single station and to take 48 samples during the fortnightly hydrographic sampling period. This frequency paralleled that used for sampling the other material classes, thus permitting easier correlations between the different material classes.

A similar analysis for nekton indicated that reduction of sampling to a single station was only 86% as effective as the three-station scheme; however, doubling the sampling frequency at this station to once every four hours could raise the overall efficiency to almost twice that of the initial effort. Biomass concentrations from A01 and A08 were significantly different; however, A05 did not differ from either of the other two (Table 4) for this variable. Station A01 was chosen as the single station for both macrozooplankton and nekton collections because the platform made this the most easily accessible location, simplified equipment and personnel logistics, and optimized work effectiveness.

TABLE 8

Relative Efficiencies (in %) of Different Combinations of Number of Stations and Number of Samples per Station for Macrozooplankton *BIOC*. -- indicates unusable combinations (too many total samples).

		NUMBER OF STATIONS			
		1	2	3	4
NUMBER OF SAMPLES:	2	7.5	11	13	14
	6	21	34	39	43
	8	33	46	52	57
	12	49	68	79	85
	14	57	80	92	100
	16	65	91	105	--
	24	98	137	--	--
	32	130	--	--	--
	48	200	--	--	--
	56	228	--	--	--

Although these site-specific conclusions were important to the overall goals of the project, the nekton and macrozooplankton data also provide ecological and life history information for different species found in the inlet and adjacent area, and illustrate the complexities of community organization and structure in a highly unstable physical environment such as a tidal pass. If estuaries serve as nursery grounds (Graham 1972) and indeed act as sources of organic materials in the form of nektonic biomass (Haedrich and Hall 1975), then these organisms must pass through tidal passes on their ways to and from the estuaries. Such questions concerning the movements of fish and other larger organisms have stimulated other investigators. Copeland (1965) first attempted to quantitatively assess the emigration of estuarine organisms through a tidal pass. Using the device from which our tide traps were ultimately derived, he found important seasonal differences in species composition and biomass, as well as considerable day-to-day

variation in the latter; however, his sampling frequency of only six times per week was too infrequent to detect much of the daily variation which we describe here. Berry and Baxter (1969) and Fore and Baxter (1972) presented data on diel fluctuations in penaeid shrimp postlarvae and larval Gulf menhaden respectively. These data, collected synoptically at 2-hour intervals over a 96-hour period, showed significant numerical differences between day and night and between ebb tide and flood tide collections, with the largest collections occurring at night during ebb tides. As in our study, periodic peaks of biomass dominated the catch statistics. Similarly, Lewis and Mann (1971) found much greater biomass concentrations for larval Atlantic menhaden at night than during the day.

Several recent papers have focused on the sources of variation in collections of ichthyoplankton and macrozooplankton. Sameoto (1975) found periodic fluctuations in zooplankton biomass related to tide. He also found significant hour-to-hour differences that exceeded those between stations, as was found in our data. In an offshore environment, Sameoto (1978) also found greater variations between tows taken at different times than between concurrent replicate tows. A time interval as short as 5 minutes produced significantly different results, demonstrating the danger of treating sequential collections as replicates. These results parallel those from the long-term nekton study where the mean value of the coefficient of variation for biomass concentration increased from 58.38 for paired replicates to 108.25 when two sets of sequential paired collections were treated as four replicates. Lee and McAlice (1979) found that tide was the dominant factor responsible for variation in zooplankton sample variation; however, different species showed different patterns between abundance and tidal height. Conte *et al.* (1979) showed that variations in density of striped bass larvae, associated with tidal stage at a single station, were greater than differences reported in the literature from geographically remote locations, which had been purported to demonstrate important environmental differences between these locations.

Our macrozooplankton data show no significant variation across the Town Creek transect with regard to total number of individuals, total biomass, or biomass concentration. This was expected considering the well-mixed physical environment of the creek (Kjerfve and Proehl 1979); however, significant cross-channel variations were present in number of species and the two diversity indices (Table 2). These variables are commonly used as measures of community diversity and considerable importance has been ascribed by some authors to variations of lesser magnitude than those reported here for a single time or for stations less than 100 m apart. Measurements of community diversity based on many samples taken within a short time period may be useful in elucidating seasonal variations (Dahlberg and Odum 1970) in community structure, while those based on data collected over long periods of time may be used to establish baseline conditions (Livingston, Kobylinski, Lewis and Sheridan 1976; Moore 1978) or to illustrate long-term and often subtle changes in communities in

response to environmental changes (McErlean, O'Connor, Mihursky and Gibson 1973; Moore 1978). Danger lies in applying importance to single measurements of diversity unless these are preceded by a thorough analysis of the normal variations in the system within the time frame of the study. We consider the diversity indices simply as indicators of community structure and associate no interpretive significance with any particular value.

Many planktonic species, including those which dominated the catch statistics, were caught only at night. This may be attributable to net avoidance during the day by the larger and more mobile organisms, as well as to known patterns of activity for many of the more abundant species (*Acetes americanus, Neomysis americanus,* portunid crab larvae, and penaeid shrimp larvae) which affect their susceptibility to capture by tidal currents or collection gear.

Significant differences for nektonic organisms were observed between all stations with respect to all dependent variables in April 1978 (Tables 3 and 4). Only one station was sampled during November 1977 when comparisons among light, time, and tidal stage produced similar results to those in April (Tables 3, 5, and 6). All variables were higher at station A01 than at either of the other stations, which were not statistically separable (Table 4). Differences in gear could have caused this, but selection by the organisms for the shallow flat (station A01) as opposed to the mid-channel or deep-channel habitats (stations A06 and A08) could account for the observed distribution of organisms. Baxter (1967), Copeland and Truitt (1966), and King (1971) reported higher concentrations of juvenile penaeid shrimp from collections made nearer the sides of channels than from those made at mid-channel locations. Simmons and Hoese (1959) noted that larger fish appear to prefer the sides of channels over mid-channel routes. King (1971) noted that red drum, *Sciaenops ocellatus,* and black drum, *Pogonias cromis,* were more abundant at a mid-channel station, whereas sheepshead, *Archosargus probatocephalus,* and flounders, *Paralichthys albigutta* and *P. lethostigma,* were more common at shoal stations. Of the 30 species of nektonic organisms collected at station A01, 18 occurred only at this station, which was located near the side of the channel. Stations A05 and A08, located at the areas of greatest depth, contributed only 10 species apiece, with only 3 and 1 species unique to each station respectively. A trend towards higher biomass values and greater numbers of organisms at the two side stations (A01 and A10) was also noted in the ichthyoplankton.

We conclude, therefore, that a preference for channel sides must exist in the highly motile nekton, but that similar preferences, if such exist in the macrozooplankton, are largely overcome by the physical mixing forces present in the creek.

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SEASONAL AND LUNAR CYCLES IN GONADOSOMATIC INDICES AND SPAWNING READINESS OF *FUNDULUS GRANDIS*

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ABSTRACT

The effects of the phases of the lunar cycle on gonadal development and spawning readiness were studied for one wild and two pond cultured populations of Gulf killifish *(Fundulus grandis).* Gonadal cycles of all three populations followed a cyclic pattern throughout the reproductive season that lasted from late February to early October. Gonads were largest and more fully developed during two peaks in the cycle, March–April and August–September. This pattern was similar in males and females, although gonad weight changes were smaller in males. No significant effect of the lunar cycle was found on gonadal maturity, although percent ripeness in males for the last quarter moon was significantly lower than that of full and new moon. Significant positive correlations were found between gonad weight and body length for all three stocks at peak spawning period. Number of ripe eggs in the females increased with body length, but there were large variations in egg numbers because of the discontinuous spawning habit of the fish. Wild fish had heavier gonads and carried more ripe eggs than their pond cultured counterparts, especially at peak spawning periods.

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INTRODUCTION

Breeding activity of Gulf killifish *(Fundulus grandis,* family Cyprinodontidae) extends from early spring to early fall along the northern Gulf coast (Simpson and Gunter 1956, Forman 1968). Under the control of several factors including temperature, photoperiod and hormonal rhythms its gonads undergo definite seasonal changes. There is current interest in the biology of *F. grandis* (called mudminnows by the bait industry in Texas) because of its use as a live bait for flounder *(Paralichthys* spp.), red drum *(Sciaenops ocellatus),* sand seatrout *(Cynoscion arenarius),* and spotted seatrout *(Cynoscion nebulosus).*

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Previously reported studies with *Fundulus notatus* (Carranza and Winn 1954), *F. heteroclitus* (Brummett 1966; Taylor, Leach, DiMichele, Livitan and Jacob 1979) and *F. majalis* (Schmelz 1970) indicate a close relationship between lunar and reproductive cycles. The following study was conducted to gather information on the reproductive biology of *F. grandis* and to determine if a relationship exists between the reproductive and lunar cycles in wild fish and fish cultured in ponds (with no tidal influence). If a cyclic response were found, it would be useful in commercial culture for the timing of mass collection of eggs.

MATERIALS AND METHODS

Field observations of a wild population of *F. grandis* were carried out in an unnamed tidal creek emptying into Trinity Bay, Texas, USA, just south of the discharge from the cooling lake that receives effluent from the Houston Lighting & Power Company's Cedar Bayou Generating Station. The creek was approximately 0.6 to 0.8 m wide with a maximum tidal-pool depth of 0.35 m at low tide. The creek and surrounding marshes were subjected to a tidal fluctuation of 0.25–0.75 m, usually once daily depending on the lunar cycle and wind direction.

Fish were trapped along the creek edge at high tide on days of new (NM), first quarter (FQ), full (FM) and last quarter (LQ) moon phases by means of 8–10 minnow traps baited with cracked crabs. Salinity (ppt), temperature (C) and water depth were recorded both when traps were set and when fish were removed. Traps were checked after 6–8 hrs when the tide began receding. Fish were tested in the field for their spawning readiness by gently pressing the abdomen from anterior to posterior. Ready release of fresh milt or mature eggs was an indicator of ripeness. Fish were transported to the laboratory where they were killed and body weight (to the nearest 0.01 g), gonad weight (wet weight to the nearest 0.001 g) and body length (SL to the nearest mm) were measured. Since *F. grandis* reach sexual maturity between 30–40 mm, only fish larger than 40 mm were included in the study. An average sample contained 20–30 fish larger than 40 mm.

Ovaries were dissected and the number of ripe eggs counted. Ripe eggs were large (1.5–2.1 mm), pale yellow translucent spheres with vacuoles concentrated at one pole, and were free in the lumen of the ovary. They were easily distinguishable from the rest of the developing ova. Any eggs expelled in the field during checks for ripeness were added to the count. Diameters of 10 unhardened, ripe eggs, freshly removed from the ovaries were measured with an ocular micrometer. Samples of fish (approximately 25 males and 25 females) were also collected on the same day as the wild fish from two 0.1 ha culture ponds at the research facility of the power plant and subjected to similar examinations. One pond contained a stock of locally acquired brood fish while the other had fish obtained from Alabama. Ponds received effluent water from the power plant. Fish were a mixture of first and second year spawners stocked at a density of 2000 per pond with an approximate sex ratio of 1 male: 1 female. Fish were fed 3% body weight per day with a commercial minnow meal containing 33% protein. A comparison of the hydrological parameters of the study site and the experimental ponds is given in Table 1.

Gonadosomatic index [GSI = (Gonad wt./Body wt.) × 100] and percent ripeness (number of ripe fish in sample as a percent of the total number) were used to document the seasonal changes of gonadal development. A three-way Analysis of Variance (ANOVA) was used to examine possible effect of the lunar phase (NM, FQ, FM and LQ), fish stock (Alabama, Texas pond or wild) and time of year on GSI and the percent ripeness of spawners (time of year was expressed as the number of moon cycles passed since study began). Each cycle was a lunar month from one new moon to the next. Percent ripeness index and GSI were subjected to angular transformation by means of the equation

$$\theta = \arcsin \sqrt{p}$$

TABLE 1

Hydrological data for the tidal creek and culture ponds recorded at the date of collecting fish samples.

Date of Sampling	Lunar Phase	Water temp. (C)		Salinity (ppt)	
		Wild	Pond	Wild	Pond
2-16-80	NM	10.4	13.5	5	7
2-23-80	FQ	15.0	15.0	5	6
3-1-80	FM	15.0	17.0	7	4
3-9-80	LQ	19.0	19.5	9	4
3-16-80	NM	19.5	18.5	7	5
3-23-80	FQ	23.0	20.0	5	6
3-31-80	FM	23.0	19.5	8	6
4-8-80	LQ				
4-15-80	NM	20.5	20.5	5	7
4-22-80	FQ	21.0	21.0	10	8
4-30-80	FM	20.0	22.0	7	8
5-7-80	LQ	24.5	24.0	7	9
5-14-80	NM	25.0	25.0	7	9
5-21-80	FQ	26.0	25.5	8	10
5-30-80	FM	27.0	27.0	11	11
6-6-80	LQ	26.0	25.5	9	12
6-13-80	NM	28.0	27.5	5	9
6-21-80	FQ	27.5	27.0	5	7
6-28-80	FM				
7-6-80	LQ	33.0	31.5	6	7
7-13-80	NM	32.0	31.0	7	8
7-21-80	FQ	25.5	30.5	8	9
7-28-80	FM	26.5	26.0	6	9
8-4-80	LQ	25.0	28.5	10	11
8-11-80	NM	30.5	29.5	10	12
8-19-80	FQ	28.0	29.0	12	14
8-27-80	FM	29.5	28.5	18	13
9-1-80	LQ	28.5	29.0	14	14
9-9-80	NM	29.0	31.0	10	12
9-17-80	FQ	26.0	24.0	10	11
9-25-80	FM	22.0	24.0	12	10

NM-New Moon, FQ-First Quarter, FM-Full Moon, LQ-Last Quarter

where θ is the value of the transformed ratio and p is the percentage. The procedure is recommended when low and high percentage values are involved (Sokal and Rohlf 1969). Regression and covariance analyses were used to investigate possible relationship between SL, gonad weight, number of ripe eggs and egg diameter. Statistical results were considered significant at the $P \leq 0.05$ level.

RESULTS

MATURATION AND SPAWNING PERIODICITY

There were distinct seasonal fluctuations in gonadal development of pond and wild fish (Figs. 1 and 2, Table 2). As revealed by the 3-way ANOVA (Table 3), fish stock and time of year had significant effects on GSI and percent

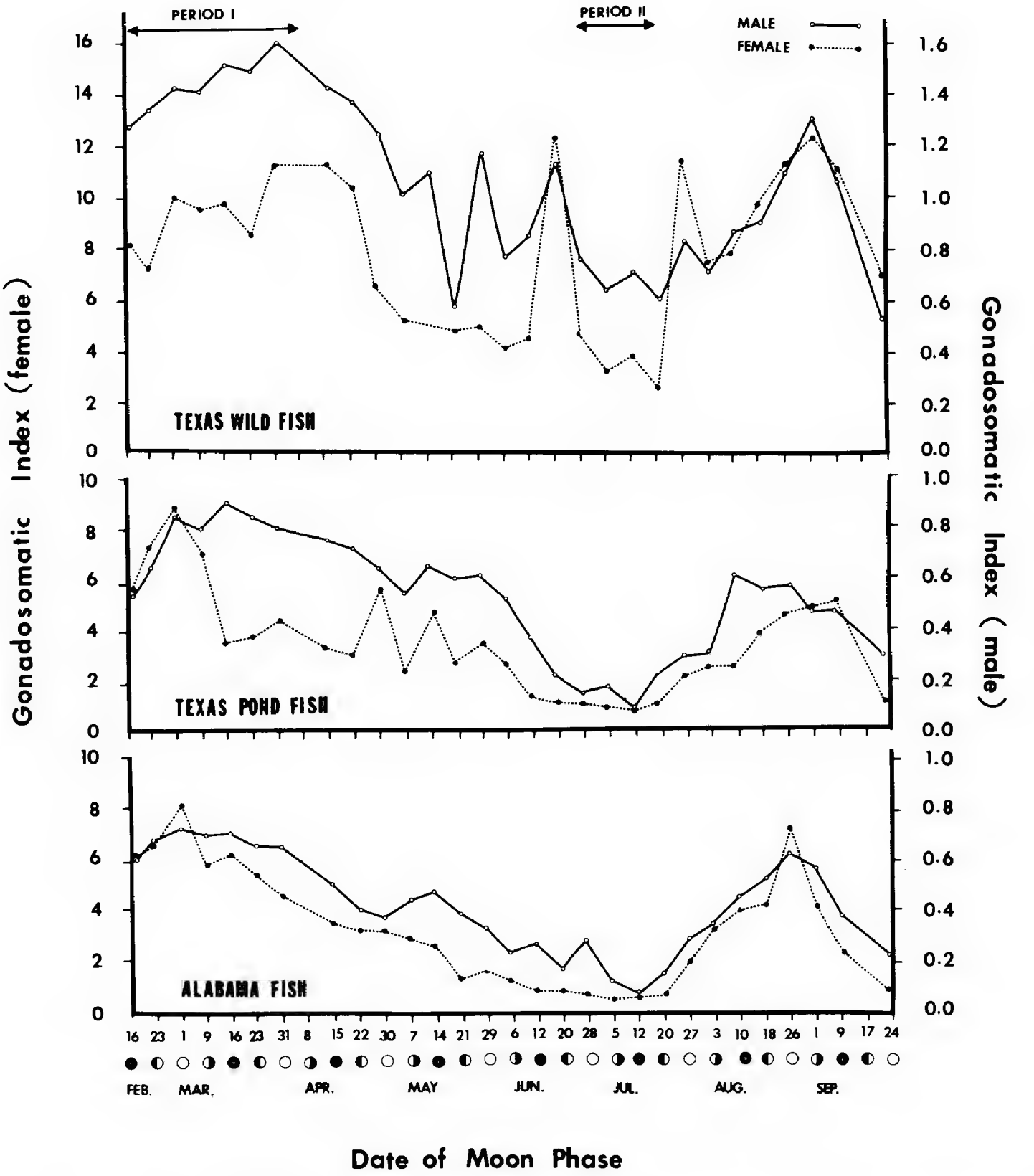
PERIOD I
PERIOD II
MALE
FEMALE
TEXAS WILD FISH
TEXAS POND FISH
ALABAMA FISH
Gonadosomatic Index (female)
Gonadosomatic Index (male)
16 23 1 9 16 23 31 8 15 22 30 7 14 21 29 6 12 20 28 5 12 20 27 3 10 18 26 1 9 17 24
FEB. MAR. APR. MAY JUN. JUL. AUG. SEP.
Date of Moon Phase

FIG. 1. Seasonal variation in gonadosomatic indices of wild and pond cultured populations of *F. grandis* over 40 mm TL. Fish were sampled within one day of moon phase. Periods I and II correspond to times of high and low egg production by pond fish.

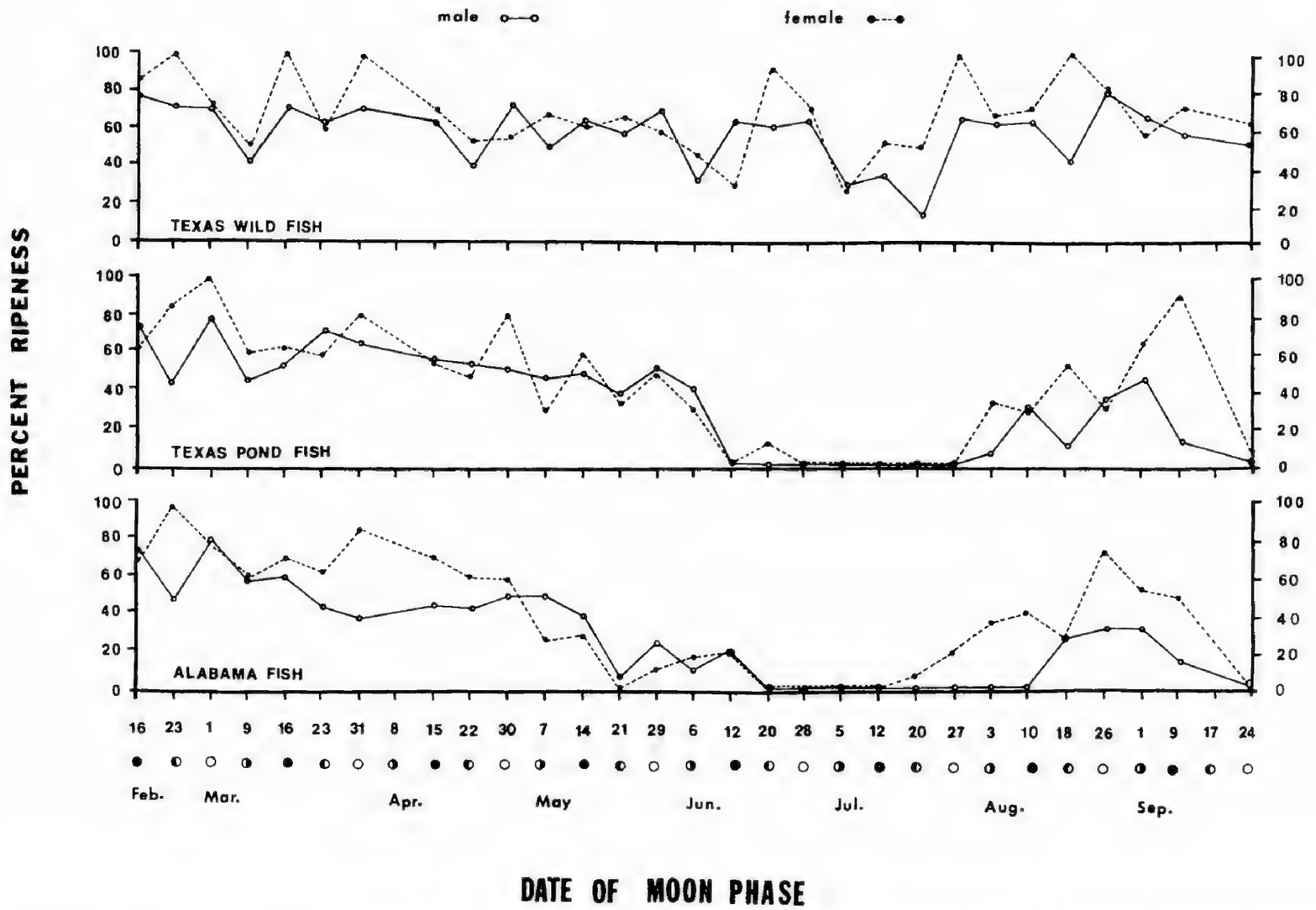
male
female
PERCENT RIPENESS
TEXAS WILD FISH
TEXAS POND FISH
ALABAMA FISH
100
80
60
40
20
0
16 23 1 9 16 23 31 8 15 22 30 7 14 21 29 6 12 20 28 5 12 20 27 3 10 18 26 1 9 17 24
Feb. Mar. Apr. May Jun. Jul. Aug. Sep.
DATE OF MOON PHASE

FIG. 2. Seasonal variation in spawning readiness (% ripe) of wild and pond cultured populations of *F. grandis* over 40 mm TL. Fish were sampled within one day of moon phase.

TABLE 2

Mean monthly GSI values for wild and pond cultured populations of *F. grandis* (Data are mean ± SE with sample sizes used for calculations in parentheses).

		Texas Pond Stock	Alabama Stock	Wild Stock
February '80	Male	0.60 ± 0.17 (37)	0.67 ± 0.17 (27)	1.33 ± 0.25 (23)
	Female	6.28 ± 2.27 (38)	6.18 ± 1.70 (33)	7.91 ± 1.75 (25)
March	Male	0.84 ± 0.29 (59)	0.70 ± 0.20 (38)	1.42 ± 0.38 (50)
	Female	5.20 ± 3.21 (34)	6.31 ± 2.42 (36)	9.36 ± 2.63 (40)
April	Male	0.70 ± 0.23 (45)	0.53 ± 0.18 (48)	1.40 ± 0.32 (38)
	Female	3.80 ± 1.55 (46)	3.61 ± 1.36 (45)	9.56 ± 2.90 (40)
May	Male	0.60 ± 0.20 (45)	0.40 ± 0.15 (42)	0.99 ± 0.30 (34)
	Female	3.45 ± 1.55 (47)	2.14 ± 1.25 (43)	5.18 ± 1.71 (42)
June	Male	0.31 ± 0.19 (45)	0.24 ± 0.22 (38)	0.89 ± 0.30 (41)
	Female	1.10 ± 0.78 (43)	0.84 ± 0.61 (40)	5.99 ± 3.63 (48)
July	Male	0.20 ± 0.13 (50)	0.16 ± 0.14 (43)	0.72 ± 0.24 (50)
	Female	1.04 ± 0.64 (51)	0.97 ± 1.26 (47)	5.72 ± 3.27 (53)
August	Male	0.50 ± 0.21 (50)	0.50 ± 0.22 (45)	0.91 ± 0.27 (39)
	Female	3.19 ± 1.76 (52)	4.94 ± 2.67 (41)	9.04 ± 3.05 (42)
September	Male	0.39 ± 0.15 (42)	0.41 ± 0.20 (41)	0.91 ± 0.43 (41)
	Female	3.27 ± 2.26 (39)	2.01 ± 1.67 (45)	9.58 ± 2.68 (36)

TABLE 3

Analysis of variance of the effect of time, fish stock and lunar phase on gonadosomatic index and spawning readiness of wild and pond cultured populations of *F. grandis*.

	Male gonadosomatic index	Female gonadosomatic index	Male percent ripeness	Female percent ripeness
Stock	$F = 241.19$ $P < 0.0001$	$F = 111.81$ $P < 0.0001$	$F = 41.16$ $P < 0.0001$	$F = 14.88$ $P < 0.0001$
Moon cycle (time)	$F = 25.98$ $P < 0.001$	$F = 12.31$ $P < 0.0001$	$F = 3.42$ $P < 0.0001$	$F = 6.85$ $P < 0.0001$
Moon phase	not significant	not significant	$F = 3.42$ $P < 0.001$	not significant
Moon cycle * Stock	not significant	$F = 2.46$ $P < 0.015$	$F = 3.35$ $P < 0.001$	not significant
Moon cycle * Moon phase	$F = 2.54$ $P < 0.008$	$F = 2.66$ $P < 0.006$	not significant	not significant
Moon phase * Stock	not significant	not significant	not significant	not significant

ripeness in both male and female spawners. There were significant interactions between time and lunar phase (moon cycle × moon phase) as

well as time and fish stock (moon cycle × stock). These were mostly due to differences in the seasonal relationships brought about by sporadic variations in GSI's, especially of Texas wild fish that occurred during late spring and early summer. Despite these interactions, the overall seasonal effects are clearly seen (Figs. 1 and 2).

There were no marked differences in temperatures between the tidal creek and ponds (Table 1). Day length for both areas was also the same. Salinity ranged from 5–18 ppt in the creek and from 4–14 ppt in the ponds (Table 1). Salinity fluctuated more among samples in the tidal creek than in ponds because of the effect of tide and surface run-off after rains.

Overall mean GSI of 1.05 for Texas wild fish was significantly higher than 0.52 and 0.43 for Texas pond and Alabama stocks, respectively. Similarly, mean female GSI of 7.67 for wild fish was significantly higher than 3.36 and 3.19 for Texas pond and Alabama females, respectively. The seasonal pattern (Fig. 1) was similar in males (M) and females (F). Peak periods of GSI were observed in the late winter and early spring and in August–September with values for wild fish much higher than for pond fish (Table 2). Maximum GSI's for pond fish (Fig. 1) were recorded during the period 16 February–16 March (Alabama M = 0.73, F = 8.23; Texas M = 0.90, F = 8.66). The spring peak in wild fish was later with highest GSI's of 1.60 and 11.04 on 31 March for males and females, respectively. Low GSI values occurred in all fish from 5–20 July when values decreased to 0.07 (M) and 0.57 (F) for Alabama, 0.07 (M) and 0.72 (F) for Texas pond and 0.63 (M) and 3.31 (F) for wild fish. Maximum GSI values were lower during the late summer peak than they were early in the breeding season except for wild females.

Changes in GSI were paralleled by a series of changes in the appearance of gonads. Active testes found in fish from March to early July were milky white and enlarged. Towards the end of the spawning season the exhausted testes regressed and became transparent and thread-like. A "ripe" ovary contained many mature eggs that gave it a granular appearance and caused it to bulge at numerous points. An exhausted ovary was small and contained yellowish, opaque, immature ova. Males and females with GSI's less than 0.2 to 2.0 respectively, typically had regressed gonads.

LUNAR EFFECT

Although plotted GSI's and percent ripeness indices seemed to indicate some variation from one lunar phase to the next in wild fish (Figs. 1 and 2), ANOVA tests failed to reveal a significant lunar effect except for male ripeness index (Table 3). Overall means for all indices averaged highest for full moon followed by new moon, first quarter and last quarter respectively (Table 4). Further evaluation using Duncan's New Multiple Range Test showed that mean percent ripeness indices for the last quarter for both males and females were significantly lower than at full and new moon (Table 4). Although this pattern was significant only for male's with regard to GSI, the general trend was the same as for percent ripeness.

TABLE 4

Results of the Duncan's New Multiple Range Test on mean male and female gonadosomatic indices and percent ripeness for the four lunar phases. Means connected by the same line are not significantly different ($P > 0.05$).

	Full moon	New moon	First quarter	Last quarter
Percentage ripeness (male)	43.56	42.38	37.42	33.94
Percentage ripeness (female)	52.83	52.51	51.12	40.31
GSI - male	0.691	0.685	0.673	0.607
GSI - female	5.06	4.76	4.70	4.34

GONAD WEIGHT AND BODY LENGTH

The relationship of gonad weight to SL was studied for two separate periods of the spawning cycle. Period I (16 February–31 March) corresponded to peak spawning while period II (28 June–20 July) corresponded to both a mid season low in egg production (Waas 1982) and few ripe fish in the ponds (Fig. 2). During both periods wild fish had heavier gonads than pond fish (Fig. 1). Significant positive correlations were found between the logarithmic values of gonad weight and SL for both males and females during period I (Table 5 and Fig. 3). The R^2 values of pond fish decreased during period II. Analysis of covariance showed that significant changes in the relationship from period I to II was brought about mainly by the decrease in gonad weight during the latter period as the gradients remained approximately the same (Table 5 and Fig. 3). In the case of Texas pond males, as shown by the negative slope of the line for period II (Fig. 3), and the positive increase in the slope of the line for period II wild females, the nature of the relationship itself changed. Covariance comparisons for these groups were thus not obtainable.

NUMBER OF RIPE EGGS AND BODY LENGTH

Linear regressions of total number of ripe ova on SL were done for the various moon cycles. The R^2 values were highest and significant for all 3 stocks only during the second moon cycle (16 March–15 April). Even during that period R^2 values were low (Fig. 4).

Based on the analysis, the number of ripe eggs increased with SL. A ripe 75 mm pond cultured female of Texas or Alabama stocks carried an average of 38 eggs at any given time during this period, while a wild fish of similar size

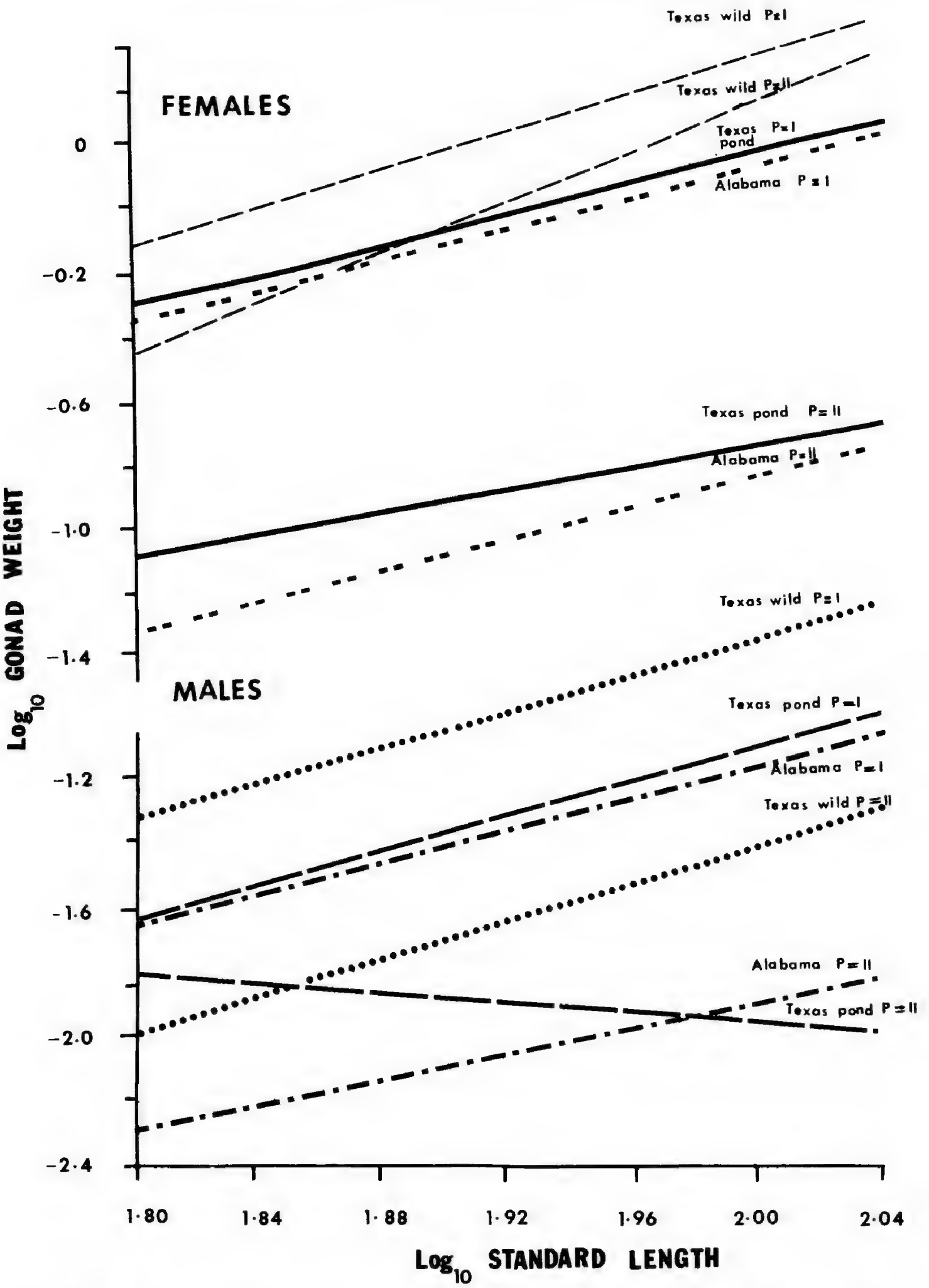

FIG. 3. The relationship of gonad weight to body length (SL) in wild and pond cultured populations of *F. grandis* during high late winter–early spring (P=I) and low summer egg production (P=II) periods of pond fish.

TABLE 5

Analyses of the regressions of $\log_{10}$ gonad weight (Y) on $\log_{10}$ standard length (X) for wild and pond cultured populations of *F. grandis* during spawning (I) and non-spawning (II) periods.

Period	Stock	Male				Female			
		n	R^2	P	Relationship	n	R^2	P	Relationship
I	Alabama	85	0.7455	$P < 0.0001$	Y= -6.1812+2.6388X	85	0.414	$P < 0.0001$	Y= -4.9988+2.4936X
	Texas Pond	105	0.6475	$P < 0.0001$	Y= -6.6194+2.9148X	103	0.5776	$P < 0.0001$	Y= -5.2017+2.603X
	Texas Wild	91	0.565	$P < 0.0001$	Y= -6.2521+2.8803X	111	0.7101	$P < 0.0001$	Y= -6.0246+3.187X
II	Alabama	59	0.1276	$P < 0.01$	Y= -5.5914+1.9502X	61	0.1838	$P < 0.0001$	Y= -8.0433+3.539X
	Texas Pond	46	0.0205	$P < 0.01$	Y= -0.6270-0.5844X	63	0.4141	$P < 0.0001$	Y= -4.6386+1.8628X
	Texas Wild	42	0.5757	$P < 0.0001$	Y= -6.7683+2.9769X	48	0.5776	$P < 0.0001$	Y= -8.3164+4.254X

carried 121. For the same period the percentages of over 40 mm females in each stock that carried ripe eggs were 67% for Texas pond (avg. 50 eggs), 73% for Alabama (avg. 47 eggs) and 64% for wild fish (avg. 130 eggs). The largest number of ripe eggs recorded during the study was found in a wild fish (98 mm SL) which carried 758.

Mean diameter of 2.09 mm for Alabama eggs was significantly higher than the 2.04 and 2.02 mm diameters for Texas wild and pond fish, respectively (Fig. 5). Egg size would effect the above relationship between body length and egg numbers since larger egg size would tend to decrease total egg count in the ovary of a large female.

DISCUSSION

Distinct seasonal fluctuations in gonadal development observed in this study with spring and late summer peaks agree with the bimodal spawning cycles reported for *F. heteroclitus* (Kneib 1976) and *F. confluentus* (Harrington 1959). High temperatures during the midspawning season were suggested as a possible cause for the summer low in spawning activity (Harrington 1959). The exact timing of the peak spawning periods is under environmental control and may vary from year to year as well as from one geographic area to another. Timing of spawning in populations of *F. heteroclitus* in the Woods Hole area was observed to be different from that in the Delaware Bay region (Wallace and Selman 1981).

Earlier work with *F. heteroclitus* (Matthews 1938; Burger 1939, 1940; Brummet 1966) and *F. confluentus* (Harrington 1959) showed seasonal changes in temperature to be the only regulator of gonadal activity in these

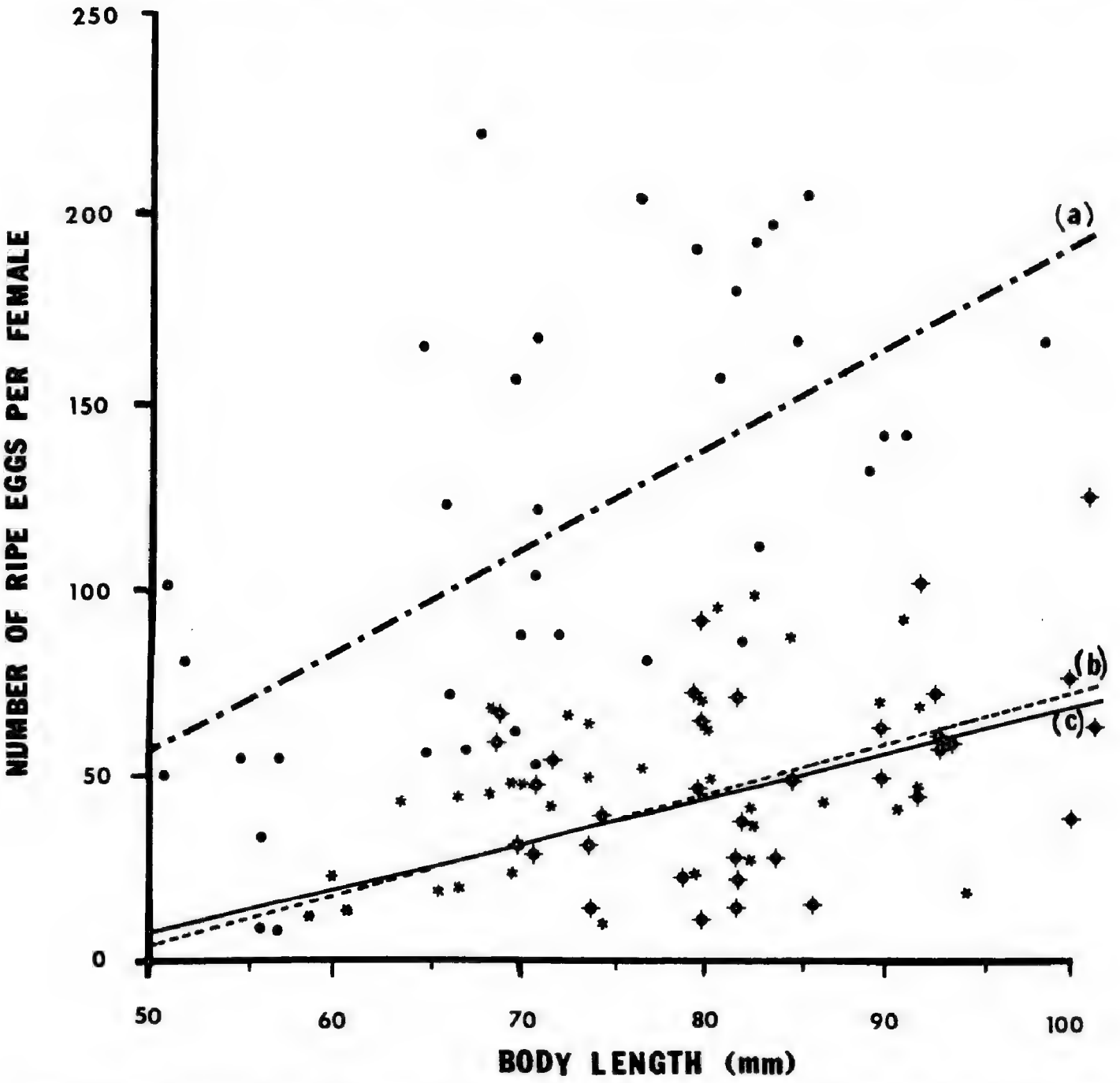

FIG. 4. The relationship between number of ripe eggs per female to SL of wild and pond cultured populations of *P. grandis* during peak spawning period. • (a) Texas wild $Y = -79..79 + 2.690X$; $R^2 = 0.28$; $P < 0.001$. ◆ (b) Texas pond $Y = -67.16 + 1.401X$; $R^2 = 0.53$; $P < 0.001$. * (c) Alabama $Y = -62.82 + 1.337X$; $R^2 = 0.23$; $P < 0.001$.

species. However, more recent work with *F. grandis* by Joseph and Meier (1971), Meier, Trobec, Joseph and John (1971), Fivizzani (1977), Spieler, Meier and Noeske (1977) and Meier, Fivizzani, Spieler and Horseman (1978) indicates that even if temperature is the dominant regulator, photoperiodic changes do exert an influence on cyclic gonadal activity via circadian mechanisms.

Daylength of approximately 11–12 hrs at which *F. grandis* started spawning (late February and early March) in our study was similar to those at which they ceased spawning in fall (October). However, temperatures at commencement of spawning (10–13 C) were much lower than at cessation of spawning (20–22 C). This indicates that time of no spawning in winter is primarily controlled by photoperiod rather than temperature.

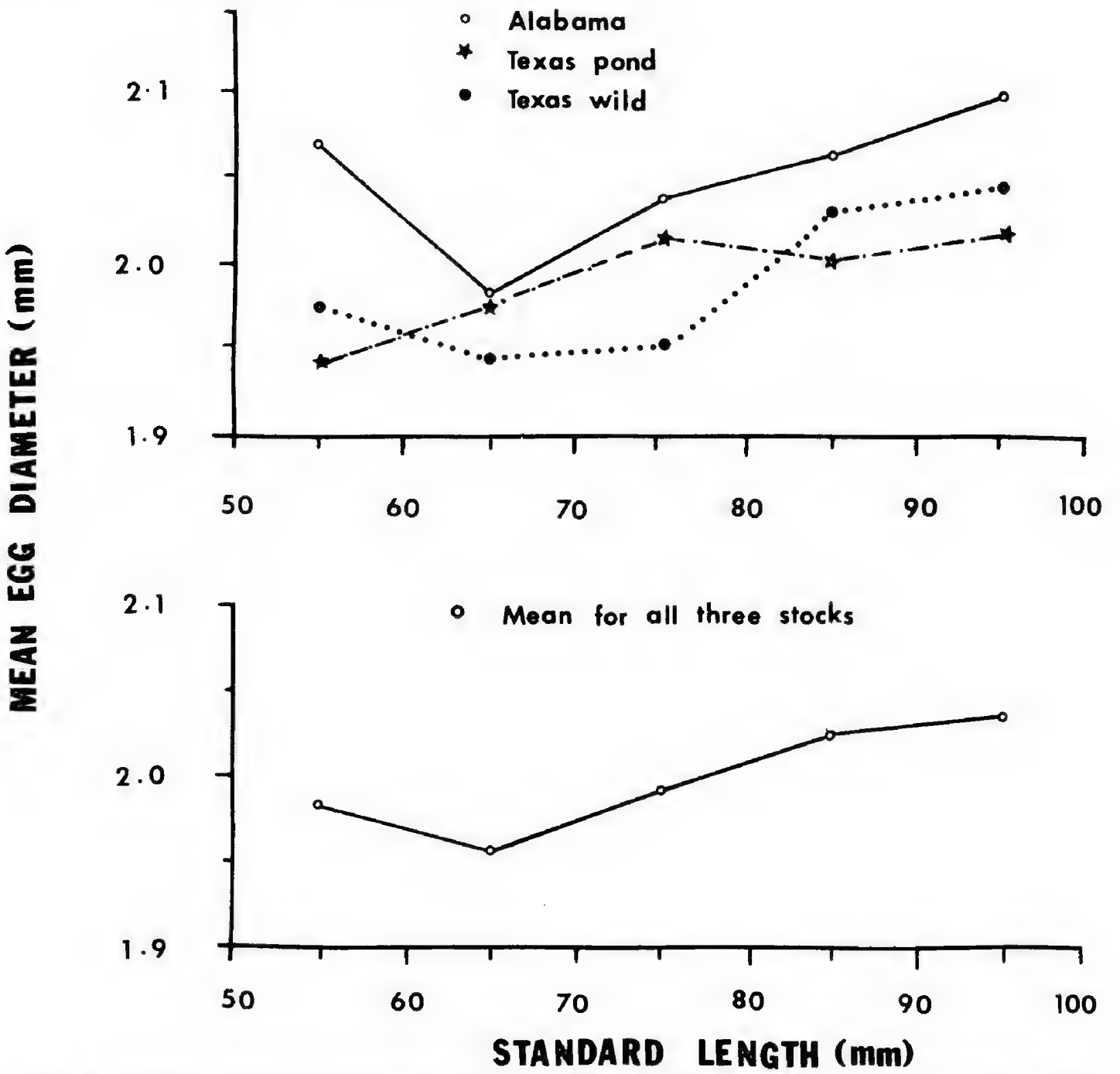

FIG. 5. Relationship of mean egg diameter and SL in wild and pond cultured populations of *F. grandis*.

Lack of significant lunar effect on the gonadal cycle may have been due, in part, to the strong effect of the wind on tidal movement along the upper Texas Gulf coast and dampening of tidal effect by the distance of the study area from the Gulf of Mexico. Tidal cycles are often overridden by strong winds. Taylor *et al.* (1979) and Taylor and Dimichele (1980) found spawning of *F. heteroclitus* in marshes of the Delaware Bay to occur during spring and summer, and in phase with spring tides of new and/or full moon. However, spawning data for pond cultured *F. grandis* in Alabama did not indicate increased activity at lunar syzygy (Trimble, Tatum and Styron 1981).

The large variation in the number of ripe ova found in females of a given length, as is evident in this study, may be caused by the discontinuous spawning habit of the fish. Little information is available on the frequency of oviposition or the number of eggs deposited at one time. Foster (1967) reported that most *Fundulus* spp. spawn 10–20 eggs at a time almost daily for

2–3 months. It was interesting to note that when females were tested for spawning readiness usually only 10–20 eggs would be readily expelled even when more ripe eggs were present in the ovary. Clusters of eggs laid on spawning mats also frequently contained 10–20 eggs. These data agree with Foster's observations. However, until frequency of spawning can be determined, actual fecundity cannot be estimated. Adult predation on eggs in the spawning mats prevented estimation of number of eggs laid through time per female.

Wild fish had heavier gonads and carried more ripe eggs than their pond cultured counterparts, especially during peak spawning periods. This indicates wild fish may lay more eggs than pond raised fish—a factor of significance from point of view of commercial culture. While there were no marked differences in temperature, salinity or photoperiod between the ponds and the wild study area, a variety of other factors may have been responsible for this difference, with nutrition, density and age of major importance. Natural environmental conditions and food may have been more conducive to gonadal development than the pond environment and artificial food. Crowding effects such as competition for nesting sites and agonistic behavior may have lessened egg production by the heavily stocked pond females. High density of pond males probably intensified spawning with the result of fewer ripe eggs retained in the ovaries of pond females than in wild females.

In the tidal marsh environment where predation pressure is high, cyprinodonts have high growth and mortality rates and the majority live only one season. (Gunter 1945; Kilby 1955). Thus, it is possible that most of the fish caught in the wild were first year spawners while those in the ponds were a mixture of first and second year spawners. Foster (1967) reported a decline in egg production with age. Large fat deposits observed as characteristic of post-reproductive females by Foster were observed in the abdominal cavities of some of the larger females particularly among pond fish. Another complication was that traps were set in a surrounding that favored presence of spawners over non-spawners.

In parameters compared in this study, Alabama and Texas stocks showed close similarity which probably indicated that it is the common pond environment that caused similarity. It is also possible that both stocks of pond fish after inbreeding may differ genetically from wild fish.

Factors effecting egg production and predation in *F. grandis* and how these factors operate in the wild and in ponds need to be investigated further to help in setting culture production goals and in increasing egg yield. It appears that only a fraction of the potential egg yield is currently being harvested from spawning ponds (Trimble *et al.* 1981, Waas 1982).

ACKNOWLEDGMENTS

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ABUNDANCE AND DISTRIBUTION OF FISHES IN THE GALVESTON BAY SYSTEM, 1963–1964[1]

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ABSTRACT

The fish fauna inhabiting the Galveston Bay estuarine system was studied from January 1963 through December 1964. Ninety-six species and 364,815 individuals were collected by trawl. Dominant in the system was *Micropogonias undulatus* (51.2% by number, 36.5% by wet weight). Other numerically important fishes were: *Anchoa mitchilli,* 22.3%; *Stellifer lanceolatus,* 8.0%; *Leiostomus xanthurus,* 4.1%; *Cynoscion arenarius,* 3.3%; and *Arius felis,* 2.4%. In terms of biomass, other important species were: *L. xanthurus,* 9.1%; *Mugil cephalus,* 7.6%; *S. lanceolatus,* 6.5%; *A. felis,* 5.7%; and *C. arenarius,* 5.0%. Fishes were most abundant in the upper estuary, while the number of species recorded was highest in the shallow Gulf of Mexico just offshore from the estuary. *Stellifer lanceolatus* was the most abundant fish in the channel zones of the estuary and co-dominated with *C. arenarius* in Gulf waters. *Anchoa mitchilli* was the dominant fish in the waters of the main tidal pass. In all other zones (open, near shore, and peripheral waters) and bay subareas, *Micropogonias undulatus* was numerically dominant. The areas of maximum abundance for 59 species are also given. Mean number of fishes per tow was significantly higher in 1963 than in 1964, attributable mainly to larger catches of *A. mitchilli* and *S. lanceolatus* in several months of 1963. However, on an annual basis, mean fish biomass per tow was stable even though monthly differences were noted.

No other system-wide studies of the fish fauna of Galveston Bay have been conducted. Results of the few limited investigations conducted before or after 1963–1964 conflict with the results of the latter. Resultant differences might equally be attributed to natural fish population fluctuations, differences in sampling methodology, and rapid human development and use of the estuary and surrounding lands.

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INTRODUCTION

In January 1963, the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) initiated a large-scale, two-year survey of the fishes, invertebrates, and hydrology of the Galveston Bay estuarine system.

[1] Contribution Number 83-21G, Southeast Fisheries Center

The object of the study was to obtain baseline ecological information on the estuary before anticipated development of land and water resources altered the area. Initial results of this study were summarized in annual reports of the Galveston Laboratory (U.S. Fish and Wildlife Service, 1964, 1965). Since the end of the survey, various aspects of the study have been examined. Pullen and Trent (1969) tabulated all hydrographic data collected in the estuary from 1958 through 1967. Pullen, Trent and Adams (1971) analyzed the temperature, salinity, nitrogen, phosphorus, and dissolved oxygen data for the 1963–1966 period. The distribution and migration of brown shrimp *(Penaeus aztecus)* were discussed by Parker (1970), and Trent, Pullen, Adams and Zamora (1974) tabulated catch per unit of effort and size of *P. aztecus* collected in the estuary from 1963 through 1967.

The only publications concerning the fishes collected in the survey have been those by Parker in 1965 and 1971. The 1965 publication is a checklist of 162 fish species recorded in the bay by the Bureau of Commercial Fisheries and the then Texas Game and Fish Commission (now Texas Parks and Wildlife Department), and the 1971 publication is a comparative analysis of the biologies of spot *(Leiostomus xanthurus)* and croaker *(Micropogonias undulatus)* in Galveston Bay and Lake Borgne, Louisiana. Bechtel and Copeland (1970), who sampled fishes at 28 sites in the estuary on a quarterly basis, related diversity to pollution inputs. No other synoptic surveys have been conducted in the Galveston Bay estuary, but several environmental impact studies of limited areal extent have been made. Reid (1955 a, b, 1956, 1957) conducted trawl surveys in three successive Junes (1954–1956) in East Bay to document the effects of the opening of Rollover Pass on the fish and invertebrate faunas. Chambers and Sparks (1959) surveyed the trawlable organisms in the San Jacinto River and the Houston Ship Channel in connection with the opening of an oil refinery. Two studies of the fish faunas near power generating stations have been conducted, one on Cedar Bayou near the mouth of the San Jacinto River (Johnson 1973) and a second near Dickinson Bay (Gallaway and Strawn 1974). The fish fauna that inhabited a dredge spoil disposal site off the mouth of Bolivar Roads Tidal Pass was examined by Henningsen (1977).

In this report, the data concerning fishes collected in the 1963–1964 estuarine survey are historically significant because of the rapid development of the surrounding areas since the time of the survey, and because the data represent a baseline for current and future research on the estuary.

MATERIALS AND METHODS

Biological sampling and water temperature and salinity data were collected at up to 65 stations in the Galveston Bay estuary of Texas from January 1963 through December 1964 (Figure 1, Table 1). Latitudes and longitudes of all stations are given in Pullen and Trent (1969). The stations were grouped by zones and subareas. Zones included:

1) Channel—9 stations, 4 to 13-m depths (mean = 11 m);
2) Open water—27 stations, 1 to 13-m depths (mean = 3 m);
3) Shore—20 stations, 0.3 to 1-m depths (mean = 0.6 m), and
4) Peripheral lakes, lagoons, and bayous—9 stations, 0.6 to 2-m depths (mean = 1.0 m).

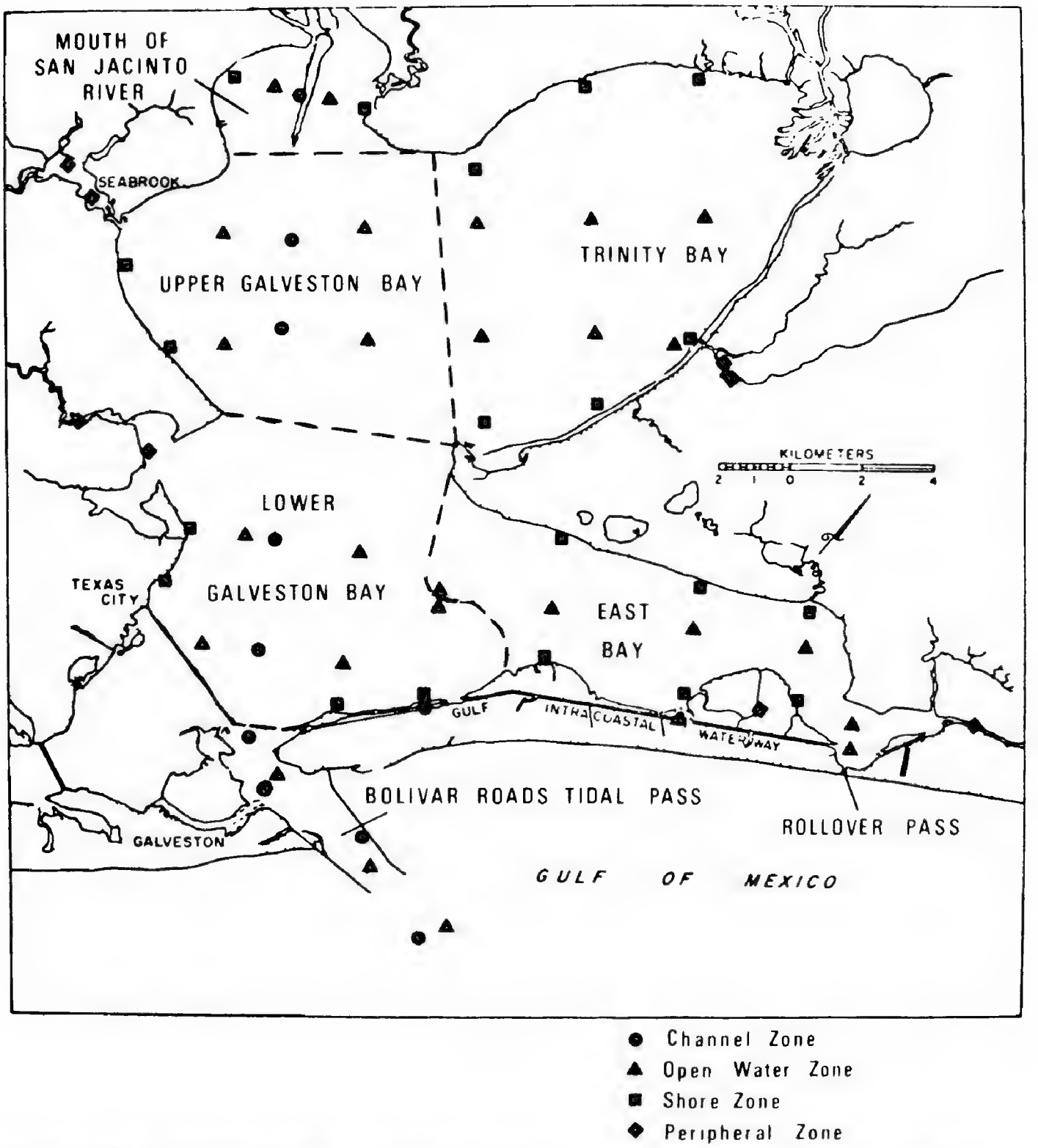

FIG. 1. The Galveston Bay system and locations of sampling stations by zones and subareas.

Subareas included: 1) Gulf of Mexico, 2) Bolivar Roads Tidal Pass, 3) Lower Galveston Bay, 4) Upper Galveston Bay, 5) Mouth of the San Jacinto River, 6) Trinity Bay, and 7) East Bay.

Data were collected twice monthly during daylight hours at each station from January 1963 through February 1964 and monthly from March through December 1964. Biological samples were collected with a 3-m otter trawl (35-mm mesh wing and body, 23-mm mesh cod end) towed for 5 minutes at about 2 knots. Fishes were returned to the laboratory where total number and wet weight were recorded for each species. Temperature and salinity were recorded from samples taken near the bottom with a Kemmerer bottle. Temperatures were measured with a stick thermometer, and salinities were measured either by Industrial Instruments Model RS-5 portable salinometer (mention of commercial products does not constitute endorsement by the U.S. Department of Commerce) or by titration of samples.

After the survey, the raw biological data were stored on computer cards which were then used to summarize the data. In the interval between data summarization and the present, the

TABLE 1

Numbers of trawls (T) and stations (N) made in various zones and subareas of Galveston Bay, 1963–1964. Zones included ship channel (C), open water (O), shore (S), and peripheral lakes, lagoons, and bayous (P). Subareas included Gulf of Mexico (GM), Bolivar Roads Tidal Pass (TP), Lower Galveston Bay (LG), Upper Galveston Bay (UG), Mouth of the San Jacinto River (MS), Trinity Bay (TB), and East Bay (EB). Station numbers are taken from Pullen and Trent (1969). Dash (–) indicated no sampling.

		Zones and Years											
		C		O		S		P		Totals		Grand	
Subarea		63	64	63	64	63	64	63	64	63	64	Total	Station Numbers
GM	T	24	14	23	14	-	-	-	-	47	28	75	1,2
	N	1		1		-		-		2			
TP	T	48	28	48	28	-	-	17	14	113	70	183	3-7
	N	2		2		-		1		5			
LG	T	72	42	118	70	93	56	48	27	331	195	526	9,16,17,24-27,32,33,
	N	3		5		4		2		14			35,36,38,44,46
UG	T	46	28	96	42	47	28	47	38	236	136	372	62-65,69,75,79,82,
	N	2		4		2		2		10			83,85
MS	T	24	14	45	28	47	28	-	-	116	70	186	95,97-100
	N	1		2		2		-		5			
TB	T	-	-	142	84	134	84	45	28	321	196	517	49-51,54,56,58,66,67,
	N	-		6		6		2		14			86-88,90,92,93
EB	T	-	-	166	98	139	84	45	28	350	210	560	11-13,18-20,22,23,28,
	N	-		7		6		2		15			29,31,39,40,42,43
Total	T	214	126	638	364	460	280	202	135				
Grand Total	T	340		1002		740		337		2419			
Total	N	9		27		20		9		65			

original data were lost. This prevented analyses of community indices such as species diversity, evenness, and similarities, for which original station data are necessary. The following sections thus deal only with summary data.

RESULTS AND DISCUSSION

THE FISH COMMUNITY

Ninety-six species of fishes were recorded among 364,815 individuals collected over the 24-month study period (Tables 2 & 3). Six species accounted for 91.3% of the total number of fishes collected: *Micropogonias undulatus,* 51.2% *Anchoa mitchilli,* 22.3%; *Stellifer lanceolatus,* 8.0%; *Leiostomus xanthurus,* 4.1%; *Cynoscion arenarius,* 3.3%; and *Arius felis,* 2.4%. *Micropogonias undulatus* was the dominant species during 14 winter through summer months, *Anchoa mitchilli* predominated during 8 fall and winter months, and *Stellifer lanceolatus* was the most abundant fish on two

TABLE 2

Monthly abundances of the 25 most numerous fishes collected in Galveston Bay in 1963 and 1964 and their distributions by zone and subarea over 24 months. Other information as in Table 1.

Temporal distribution: Species	1963 Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Micropogonias undulatus	3125	4743	23310	36608	36309	12360	4685	1734	379	208	573	934
Anchoa mitchilli	1851	5498	3550	4332	6109	9960	2886	3382	4154	10220	5815	3308
Stellifer lanceolatus	16	1	6	52	130	1656	3202	16901	1013	914	683	201
Leiostomus xanthurus	150	110	153	918	1968	973	1309	752	294	156	75	401
Cynoscion arenarius	19	6	52	347	1165	862	951	1137	464	1236	393	151
Arius felis	10	1	21	34	39	38	285	3436	1457	1016	52	9
Sphoeroides parvus	45	1	61	70	283	717	750	974	470	196	248	263
Brevoortia patronus	149	225	1561	163	85	288	28	17	17	25	57	277
Symphurus plagiusa	102	242	224	132	188	228	103	165	173	206	300	404
Citharichthys spilopterus	9	19	8	113	1252	705	428	227	79	35	31	15
Polydactylus octonemus			4	87	598	517	150	38	8			
Menticirrhus americanus	42	35	299	18	107	69	55	40	89	70	54	280
Mugil cephalus	149	322	83	36	8	2	10	9	2	2	3	292
Bagre marinus					1	1	166	333	45	16		
Achirus lineatus	11			2		3	44	152	80	117	145	31
Prionotus tribulus	71	38	131	83	40	18	7	2		18	20	54
Etropus crossotus	19		16	11	4	4	42	53	74	36	58	70
Porichthys plectrodon			2	8	21	41	16	21	28	128	26	5
Paralichthys lethostigma	38	29	43	62	30	5	7	7	7	3	9	4
Urophycis floridanus	4	7	36	9								2
Bairdiella chrysoura	1	2	4	4	15	18	25	18	13	3	3	7
Chaetodipterus faber	1			1	2	4	8	19	29	24	10	7
Cyprinodon variegatus	67	17										13
Synodus foetens	1				16	3	18	14	21	34	23	8
Larimus fasciatus		2	3	3	9	13	3		4	18	20	2
Total number of individuals	6082	11445	29698	43146	48432	28542	15235	29569	9007	14774	8688	6907
Total number of species	46	41	45	41	42	44	45	48	49	44	46	50
Total number of trawl tows	110	115	126	128	130	129	129	130	130	130	128	129

Temporal distribution: Species	1964 Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Micropogonias undulatus	740	4469	10181	13887	15919	8046	4140	1223	472	235	1121	1421
Anchoa mitchilli	1745	1184	1336	814	2393	544	669	296	391	5564	4030	1144
Stellifer lanceolatus	30	39	13	52	47	759	1237	881	758	342	241	93
Leiostomus xanthurus	46	81	175	765	2642	1457	1031	644	403	210	155	111
Cynoscion arenarius	5	13	8	20	1479	1045	1102	614	278	288	181	111
Arius felis			78	9	14	33	122	512	473	472	792	25
Sphoeroides parvus	2	38	63	22	36	297	451	199	276	227	298	316
Brevoortia patronus	153	579	156	190	127	237	55	26	119	22	40	133
Symphurus plagiusa	354	197	89	118	65	78	114	64	66	102	246	356
Citharichthys spilopterus			7	6	233	326	162	56	29	8	6	1
Polydactylus octonemus	2		1	48	654	33	77	4				
Menticirrhus americanus	20	38	20	15	14	28	32	15	23	104	59	98
Mugil cephalus	282	300	5	7	4	6	9	8	2	7	2	39
Bagre marinus							35	319	88	17		
Achirus lineatus	1						1	10	40	24	18	22
Prionotus tribulus	23	14	34	27	36	8	11	4	3	15	21	19
Etropus crossotus	6	2	1	1	1	11	25	33	18	46	63	53
Porichthys plectrodon			1	4	5	8	15	13	8	21	13	1
Paralichthys lethostigma	6	8	5	45	2	7	8	1	3	1	4	11
Urophycis floridanus	1	72	91	51			1					
Bairdiella chrysoura	2	3	1			3	5	94	20	1	3	14
Chaetodipterus faber				1	4	1	18	27	18	9	7	5
Cyprinodon variegatus	81	7										6
Synodus foetens			1		5	1	4	6	4	5	8	2
Larimus fasciatus	18	11	1	5	7	2	13	1		2	5	
Total number of individuals	3646	7172	12299	16115	23758	12960	9452	5081	3566	7830	7348	4063
Total number of species	39	37	36	33	37	36	46	36	36	39	34	47
Total number of trawl tows	128	128	65	65	65	65	65	65	65	65	65	64

TABLE 2 (Continued)

Areal distribution: Species	2-yr Total	Zone				Subarea						
		C	O	S	P	GM	TP	LG	UG	MS	TB	EB
Micropogonias undulatus	186822	11348	77858	57768	39848	1140	2442	22569	22207	18462	50767	69235
Anchoa mitchilli	81175	2436	44926	21959	11854	544	3295	18272	14540	5080	24479	14965
Stellifer lanceolatus	29267	24548	4041	456	222	1359	614	15506	8991	1619	248	930
Leiostomus xanthurus	14979	224	1561	7816	5378	91	312	1411	1226	1338	3167	7434
Cynoscion arenarius	11927	1617	6375	1731	2204	1345	804	2665	1500	688	1835	3090
Arius felis	8928	987	2550	4809	582	26	265	1703	2764	1565	1623	982
Sphoeroides parvus	6303	224	2550	3095	434	72	398	438	902	2100	1603	790
Brevoortia patronus	4729	315	763	2708	943	5	36	186	739	541	1011	2211
Symphurus plagiusa	4316	2592	992	199	533	458	316	957	1230	662	175	518
Citharichthys spilopterus	3755	255	1799	649	1052	84	185	919	549	61	626	1331
Polydactylus octonemus	2221	1019	879	260	63	168	1312	319	153	103	29	137
Menticirrhus americanus	1624	579	517	512	16	182	540	484	120	16	41	241
Mugil cephalus	1589	1	167	342	1079		23	91	196	57	289	933
Bagre marinus	1021	133	394	339	155		7	73	259	150	335	197
Achirus lineatus	701	43	234	52	372	2	10	108	96	39	157	289
Prionotus tribulus	697	131	293	205	68	98	75	116	122	72	95	119
Etropus crossotus	647	153	346	131	17	56	57	291	79	19	31	114
Porichthys plectrodon	385	109	188	38	50	65	16	106	66	14	72	46
Paralichthys lethostigma	345	11	32	48	254		11	69	67		48	150
Urophycis floridanus	274	183	53	9	29	21	22	46	99	44	1	41
Bairdiella chrysoura	259	100	75	60	24	4	16	114	32	14	27	52
Chaetodipterus faber	195	49	48	63	35	5	12	65	16	27	24	46
Cyprinodon variegatus	191	1	12	24	154			9	2	6	2	172
Synodus foetens	174	13	69	52	40	5	35	46	25		12	51
Larimus fasciatus	142	50	91	1		54	79	3			1	5
Total number of individuals	364815	47533	147435	103853	65994	5913	11159	67069	56230	32796	87071	104577
Total number of species	96	65	80	74	73	47	50	76	57	47	61	70
Total number of trawl tows	2419	340	1002	740	337	75	183	526	372	186	517	560

late summer occasions. Parker (1971) gives a thorough treatment of the abundance and distribution of *Micropogonias undulatus* and *Leiostomus xanthurus. Cynoscion arenarius* and *Leiostomus xanthurus* were generally most abundant in spring and summer while *Arius felis* peaked in summer and fall. Other numerous species which showed seasonal abundance peaks included: *Symphurus plagiusa* and *Mugil cephalus* in winter; *Brevoortia patronus, Citharichthys spilopterus,* and *Polydactylus octonemus* in spring; *Sphoeroides parvus, Bagre marinus,* and *Achirus lineatus* in summer; and *Etropus crossotus* and *Porichthys plectrodon* in fall.

Fishes were generally most abundant in April and May and least abundant in December and January (Table 2). More species were collected in December of each year than in other months, although the monthly variation (taking into account the number of tows per month) was not great—41 to 50 species in 1963, 33 to 47 species in 1964.

Collections were grouped according to zones and subareas (Table 2). The peripheral zone yielded the greatest number of individuals per tow (N/T) over the study period: N/T = 195.8, 147.1, 140.3, and 139.8 for peripheral, open water, shore, and channel zones, respectively. Species per tow (S/T) were higher in peripheral (0.22) and channel (0.19) zones than inshore (0.10) and open water (0.08) zones. With respect to subareas, fishes were more abundant in the East Bay, San Jacinto River, Trinity Bay, and Upper Galveston Bay subareas (N/T = 186.7, 176.3, 168.4, and 151.2, respectively) and distinctly less abundant in Lower Galveston Bay, the Gulf of Mexico, and the Tidal Pass (N/T = 127.5, 78.8, and 61.0, respectively). Species were by far more numerous in the Gulf subarea (S/T = 0.63) than elsewhere (S/T = 0.12 to 0.27). *Stellifer lanceolatus* was the most abundant species in the

TABLE 3

Total abundances of species which occurred in Galveston Bay in 1963–1964 and which are not listed in Table 2.

Species	No.	Species	No.
Gobiosoma bosci	126	*Syngnathus scovelli*	13
Trinectes maculatus	126	*Ictalurus punctatus*	13
Lagodon rhomboides	120	*Gobionellus boleosoma*	12
Gobiesox strumosus	107	*Membras martinica*	12
Menidia beryllina	107	*Microgobius gulosus*	12
Myrophis punctatus	88	*Hypsoblennius ionthas*	11
Dorosoma cepedianum	88	*Chilomycterus schoepfi*	8
Pogonias cromis	81	*Elops saurus*	7
Mugil curema	77	*Harengula jaguana*	6
Chloroscombrus chrysurus	72	*Hemicaranx amblyrhynchus*	6
Orthopristis chrysoptera	71	*Peprilus paru*	5
Dorosoma petenense	68	*Caranx bartholomaei*	4
Oligoplites saurus	62	*Chaenobryttus gulosus*	4
Peprilus burti	57	*Ictiobus bubalus*	4
Cynoscion nebulosus	56	*Chasmodes bosquianus*	3
Eucinostomus gula	53	*Dormitator maculatus*	3
Ancylopsetta quadrocellata	50	*Lepisosteus spatula*	3
Gobionellus hastatus	49	*Monacanthus hispidus*	3
Sciaenops ocellatus	45	*Opisthonema oglinum*	3
Fundulus similis	44	*Selene setapinnis*	3
Dasyatis sabina	40	*Gymnothorax moringua*	2
Archosargus probatocephalus	39	*Lepisosteus osseus*	2
Centropristis philadelphica	37	*Lutjanus synagris*	2
Ophichthus gomesi	37	*Poecilia latipinna*	2
Syngnathus floridanus	37	*Selene vomer*	2
Astroscopus y-graecum	36	*Cyprinus carpio*	1
Ictalurus furcatus	32	*Dasyatis sayi*	1
Fundulus grandis	28	*Gobionellus shufeldti*	1
Anchoa hepsetus	27	*Hippocampus zosterae*	1
Caranx hippos	26	*Lepomis macrochirus*	1
Microgobius thalassinus	21	*Ogcocephalus radiatus*	1
Lepisosteus oculatus	20	*Raja texana*	1
Opsanus beta	19	*Scorpaena calcarata*	1
Cynoscion nothus	19	*Seriola rivoliana*	1
Trichiurus lepturus	15	*Trachinotus carolinus*	1
Prionotus scitulus	14		

channel zone and co-dominated with *Cynoscion arenarius* in the Gulf subarea. *Micropogonias undulatus* predominated in all other zones and subareas except in the Tidal Pass, where *Anchoa mitchilli* was the most numerous species.

SEASONALITY

The fish communities in the various zones and subareas demonstrated several seasonal trends in both mean total numbers per tow and mean total biomass per tow (B/T). In the peripheral zone, fishes were most numerous in March, yet biomass peaks were found in April–May and August (Figure 2).

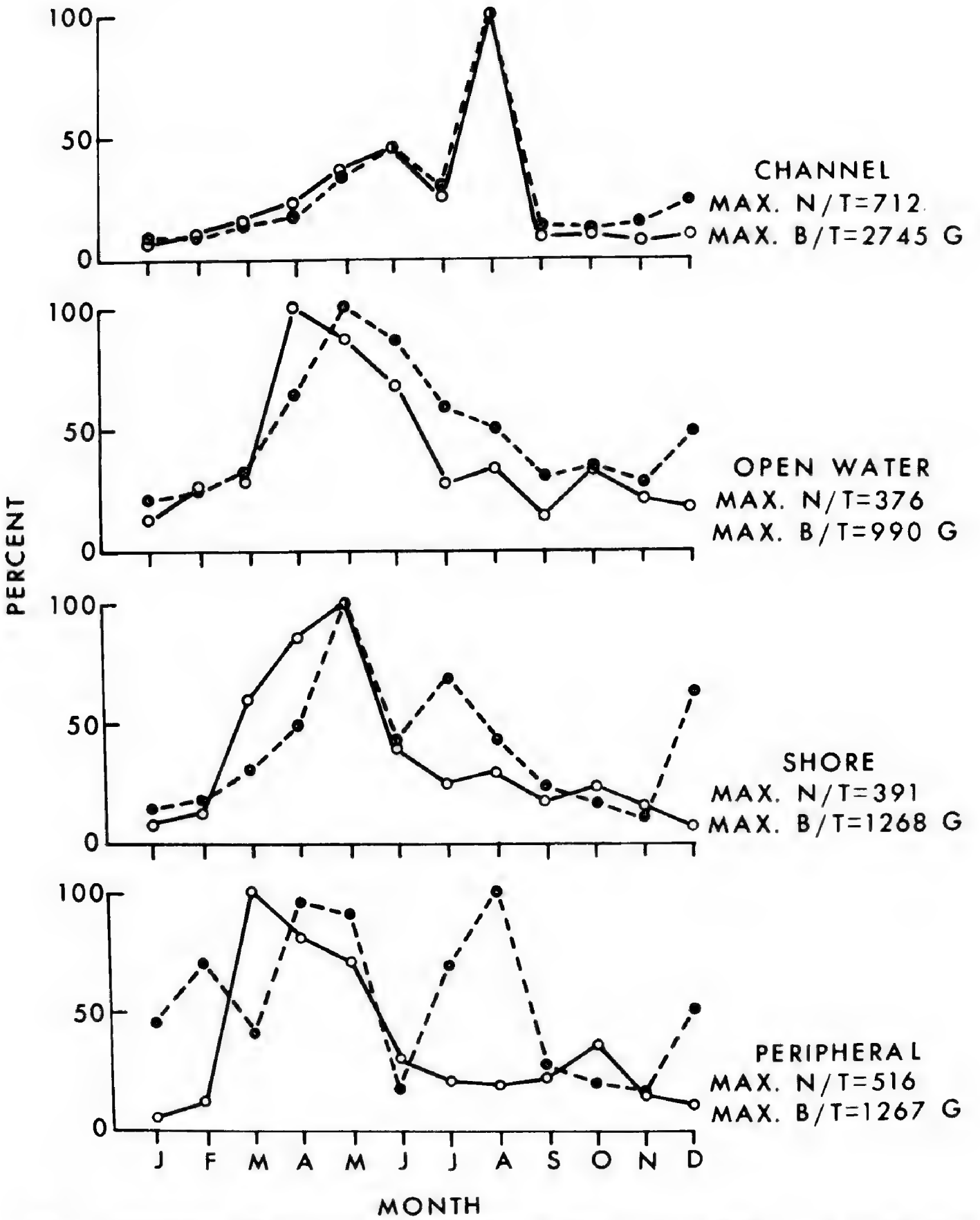

FIG. 2. Percentage of maximum mean monthly number per tow (N/T, —o—) and biomass per tow (B/T, --●--) for all fishes by Galveston Bay depth zone.

In the shore zone, both numbers and biomass peaked in May, while in the open water zone, numbers peaked in April and biomass peaked in May. Both numbers and biomass of fishes in the channel zone were at a maximum in August. The seasonal variations of N/T and B/T within each zone were significantly ($P<0.05$) correlated in the channel, open water, and shore

zones, but not in the peripheral zone. Inter-zone comparison of N/T and B/T (Table 4) showed significant ($P<0.05$) correlations in N/T trends among all

TABLE 4

Matrices of correlation coefficients comparing mean monthly number and biomass of fishes per tow (N/T and B/T, respectively) in zones and subareas of Galveston Bay, 1963–1964. Significant correlations ($P < .05$) are indicated by asterisks (*). Other information is given in Table 1.

		Zones				
		C	O	S	P	
	C		.441	.374	.359	
	O	.334		.854*	.374	B/T
N/T	S	.283	.877*		.336	
	P	.096	.526*	.776*		

		Subareas						
		GM	TP	LG	UG	MS	TB	EB	
	GM		.837*	.012	.271	.331	.668*	.503*	
	TP	.745*		.069	.282	.474	.722*	.584*	
	LG	.174	.207		.608*	.340	.297	.267	B/T
N/T	UG	.365	.436	.721*		.338	.605*	.419	
	MS	.254	.466	.366	.618*		.573*	.729*	
	TB	.634*	.807*	.276	.717*	.662*		.438	
	EB	.272	.462	.291	.713*	.873*	.821*		

but the channel zone, while B/T trends were only correlated in the open water and shore zones. Within each subarea, seasonal variations in N/T and B/T were significantly ($P<0.05$) correlated in all but East Bay (Figures 3–4). Maximum numbers of fishes were collected during April in East Bay and the mouth of the San Jacinto River, during May in Trinity Bay and the Tidal Pass, during June in the Gulf waters, and during August in Lower Galveston Bay. A bimodal trend was found in Upper Galveston Bay, where abundance peaks were found in April and August. Comparisons of N/T and B/T between subareas (Table 4) demonstrated that adjoining subareas generally had similar trends in numbers of fishes (excepting Lower Galveston Bay), and that biomass trends were not as well linked. The N/T and B/T trends in the Trinity Bay subarea were correlated with most other subareas, while those in the Lower Galveston Bay subarea were correlated only with Upper Galveston Bay.

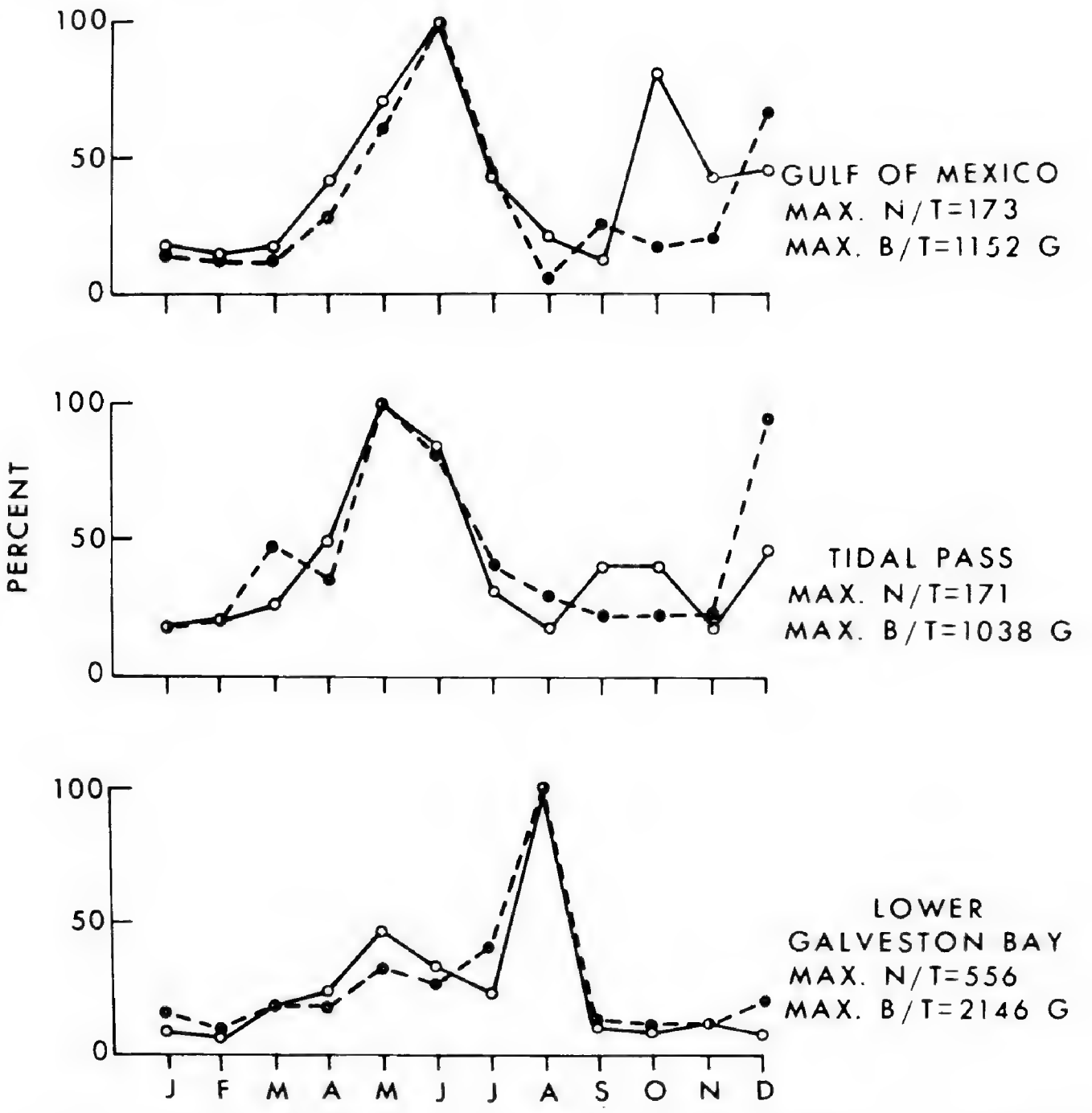

FIG. 3. Percentage of maximum mean monthly number per tow (N/T, —o—) and biomass per tow (B/T, --●--) for all fishes by Galveston Bay subarea.

NUMERICAL ABUNDANCE

The overall distributions of the six most numerous fishes and of the total fish fauna by zone and subarea are summarized in Table 5. *Micropogonias undulatus* was generally most numerous in the peripheral zone of each subarea and in the lower salinity subareas of each zone. Its peak abundance was in the peripheral zone of East Bay (N/T = 235.2), where the total fish fauna was also highest (N/T = 397.8). *Anchoa mitchilli* tended to be more numerous in the open water zones of mid-estuary and in the peripheral zones of the lower salinity subareas. *Anchoa mitchilli* was most abundant in the open waters of Upper Galveston Bay (N/T = 77.2) and in the peripheral waters of Trinity Bay (N/T = 71.2). *Stellifer lanceolatus* occurred primarily in the channel zones of Upper and Lower Galveston Bay (N/T = 115.8 and 116.4). *Leiostomus xanthurus* was most abundant in the peripheral zone of

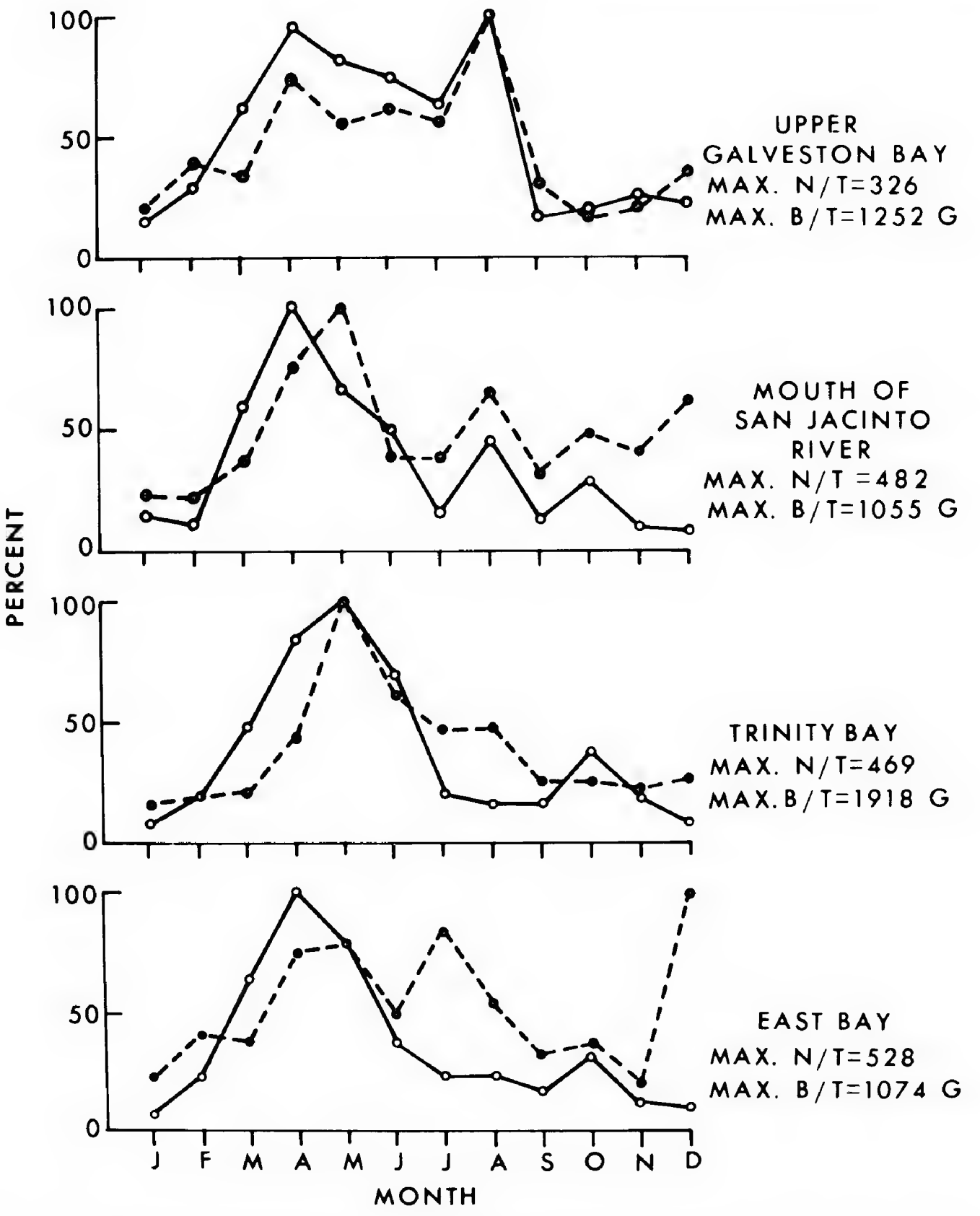

FIG. 4. Percentage of maximum mean monthly number per tow (N/T, —o—) and biomass per tow (B/T, --●--) for all fishes by Galveston Bay subarea.

East Bay (N/T = 54.5). *Cynoscion arenarius* was collected primarily in the channel and open water zones of the Gulf of Mexico (N/T = 13.7 and 22.3) and in the peripheral zone of East Bay (N/T = 18.1). *Arius felis* occurred most frequently in the shore zones of Upper Galveston Bay and the mouth of the San Jacinto River (N/T = 21.0 and 13.8).

The abundance patterns of *M. undulatus, L. xanthurus,* and *C. arenarius* were highly correlated between the two years of sampling (Table 6). These

TABLE 5

Mean number of fishes per tow (N/T) in zone-subarea combinations for the six most abundant fishes and the total fish fauna in Galveston Bay, 1963–1964.Asterisk (*) indicates the dominant fish in each combination. Other information is given in Table 1.

Subarea	Zone C	Zone O	Zone S	Zone P	Subarea	Zone C	Zone O	Zone S	Zone P
		M. undulatus					*A. mitchilli*		
GM	17.8	12.6	-	-	GM	9.3	5.1	-	-
TP	16.8*	12.6	-	6.8	TP	15.8	13.1*	-	35.4*
LG	22.8	38.9	36.7	95.8*	LG	2.3	59.9*	38.4*	13.8
UG	59.9	62.2	38.1*	74.6*	UG	6.3	77.2*	28.2	15.4
MS	62.5*	136.6*	81.5*	-	MS	4.0	37.3	29.4	-
TB	-	109.8*	78.0*	122.5*	TB	-	53.6	32.9	71.2
EB	-	97.5*	118.0*	235.2*	EB	-	26.7	21.2	44.1
		S. lanceolatus					*L. xanthurus*		
GM	22.0*	14.1	-	-	GM	1.1	1.4	-	-
TP	5.0	3.0	-	<0.1	TP	0.4	1.9	-	4.3
LG	116.4*	11.7	0.2	0.1	LG	0.2	0.6	3.5	9.9
UG	115.8*	2.6	0.9	<0.1	UG	1.2	1.0	7.2	5.4
MS	39.2	0.9	0.9	-	MS	1.1	3.9	13.5	-
TB	-	1.0	0.1	0.0	TB	-	0.7	13.5	1.0
EB	-	1.7	1.2	1.9	EB	-	2.5	12.5	54.4
		C. arenarius					*A. felis*		
GM	13.7	22.3*	-	-	GM	0.5	0.2	-	-
TP	4.3	4.4	-	4.5	TP	0.5	2.2	-	2.0
LG	2.8	9.6	1.7	3.8	LG	4.9	0.9	5.2	2.7
UG	4.5	5.6	1.9	2.9	UG	3.9	5.2	21.0	2.1
MS	3.0	3.9	3.9	-	MS	2.3	6.0	13.8	-
TB	-	5.2	2.1	2.8	TB	-	3.4	3.9	0.2
EB	-	4.4	2.7	18.1	EB	-	1.1	2.6	0.5
		All Fishes							
GM	87.0	70.5	-	-					
TP	63.9	59.2	-	58.1					
LG	161.6	130.9	93.8	134.1					
UG	211.4	162.7	109.6	116.7					
MS	139.8	206.1	165.8	-					
TB	-	182.9	140.2	207.9					
EB	-	140.3	173.3	397.8					

three dominants plus *A. felis* demonstrated similar mean N/T values when summed over all stations and months in each year, even though there were instances of significant differences in N/T values between similar months in successive years. This was not the case for *A. mitchilli* and *S. lanceolatus,* both of which showed distinctive abundance patterns in successive years and higher overall N/T values in 1963. In all but 2 months, the 1963 system-wide N/T values for *A. mitchilli* exceeded those in 1964, significantly so in six of those months. The differences in *S. lanceolatus* abundance were mainly attributable to a single month (August 1963) when an extremely large catch was recorded. Although the N/T values for the total fish fauna showed a high degree of regularity between years, the catch was significantly higher in

TABLE 6

Comparison of monthly and yearly mean number of fishes per tow (N/T) collected over all stations for the six most numerous fishes and the total fish fauna in Galveston Bay, 1963–1964. Asterisk (*) indicates both significant differences (χ^2, $P < .05$) between corresponding months in each year and significant correlations (r, $P < .05$) in trends between years.

	YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN-DEC	r
Micropogonias undulatus	1963	28.4*	41.2	185.0	286.0*	279.3	95.8	36.3	13.3	2.9	1.6	4.5	7.2	82.5	.977*
	1964	5.8	34.9	156.6	213.6	244.9	123.8*	63.7*	18.8	7.3	3.6	17.2*	22.2*	68.3	
Anchoa mitchilli	1963	16.8	47.8*	28.2	33.8*	47.0	77.2*	22.4*	26.0*	32.0*	78.6	45.4	25.6	40.3*	.546
	1964	13.6	9.3	20.6	12.5	36.8	8.4	10.3	4.6	6.0	85.6	62.0	17.9	22.2	
Stellifer lanceolatus	1963	0.1	0.1	0.1	0.4	1.0	12.8	24.8	130.0*	7.8	7.0	5.3	1.6	16.4*	.465
	1964	0.2	0.3	0.2	0.8	0.7	11.7	19.0	13.6	11.7	5.3	3.7	1.5	5.0	
Leiostomus xanthurus	1963	1.4	1.0	1.2	7.2	15.1	7.5	10.1	5.8	2.3	1.2	0.6	3.1	4.8	.942*
	1964	0.4	0.6	2.7	11.8	40.6*	22.4*	15.9	9.9	6.2	3.2	2.4	1.7	8.5	
Cynoscion arenarius	1963	0.2	0.1	0.4	2.7	9.0	6.7	7.4	8.7	3.6	9.5	3.1	1.2	4.5	.764*
	1964	0.1	0.1	0.1	0.3	22.8*	16.1*	12.0	9.4	4.3	4.4	2.8	1.7	5.7	
Arius felis	1963	0.1	0.1	0.2	0.3	0.3	0.3	2.2	26.4*	11.2	7.8	0.4	0.1	4.2	.535
	1964	0.0	0.0	1.2	0.1	0.2	0.5	1.9	7.9	7.3	7.3	12.2*	0.4	2.8	
Total Fishes	1963	55.3*	99.5*	235.7*	337.1*	372.6	221.3	118.1	227.5*	69.3	113.6	67.9	53.5	166.1*	.881*
	1964	28.5	56.0	189.2	247.9	365.5	199.4	145.4	78.2	54.9	120.5	113.0*	63.5	125.2	

1963 and was particularly so in the January-April collections. If either the high 1963 *A. mitchilli* or *S. lanceolatus* catches were regarded as abnormal and were adjusted downward to 1964 catch rates, then the overall N/T for the total fish faunas in 1963 and 1964 would not be significantly different.

Comparison of annual N/T values between years for the total fish faunas found in the various zone-subarea combinations (Table 7) demonstrated the fluctuating abundances in local fish faunas and the effects of the dominant species on local catch rates. In most cases, catches were higher in 1963 than in 1964. *Stellifer lanceolatus, A. mitchilli,* and *M. undulatus* populations were most responsible for local catch differences, although in some instances (*e.g.,* channel zone of the Gulf of Mexico) changes in fish catch were due to an overall increase (or decrease) in all fishes collected.

The areas of maximum abundance of 59 fishes over the 24-month period are presented in Table 8, along with the dominant fish in each zone-subarea combination. Thirty-seven species were not abundant enough to determine such information. Most species had maximum N/T values of less than 5, aside from the previously discussed dominants. The exceptions included: *Polydactylus octonemus,* N/T = 10.3 in the channel zone of the Tidal Pass; *Symphurus plagiusa,* N/T = 14.5 in the channel zone near the San Jacinto River; *Sphoeroides parvus,* N/T = 16.2 in the shore zone of the San Jacinto River; *Brevoortia patronus,* N/T = 8.0 in the shore zone of East Bay; and *Mugil cephalus,* N/T = 10.0 and *Citharichthys spilopterus,* N/T = 8.2 in the peripheral zone of East Bay.

BIOMASS

Seven fishes, including the six numerical dominants, comprised 73.8% of the total biomass (Table 9). *Micropogonias undulatus* was by far the

TABLE 7

Comparison of 1963 and 1964 annual mean number of fishes per tow (N/T) by zone and subarea in Galveston Bay, Texas. Species whose annual fluctuations in abundance most affected the N/T values are indicated by superscripts as follows: 1= *Stellifer,* 2=*Anchoa mitchilli,* 3=*Micropogonias,* 4=*Arius,* 5=*Brevoortia,* 6=*Leiostomus.* Other information as in Table 1.

		ZONE			
Subarea	Yr	C	O	S	P
GM	63	73.2	66.8	-	-
	64	110.5	76.6	-	-
TP	63	66.8	56.7	-	100.8^{2}
	64	59.0	63.4	-	6.2
LG	63	222.9^{1}	149.5^{2}	107.7^{23}	130.2
	64	56.6	99.5	70.8	140.9
UG	63	254.8^{1}	167.9	136.5^{234}	90.6
	64	140.1	150.9	64.5	148.5^{3}
MS	63	148.9^{1}	274.3^{3}	189.4^{23}	-
	64	124.2	96.5	126.1	-
TB	63	-	204.8^{2}	121.5_{2356}	227.0^{2}
	64	-	145.9	170.1^{2356}	177.3
EB	63	-	168.9^{3}	187.5^{35}	390.9
	64	-	91.9	149.7	408.9

dominant fish with 36.5% of the 24-month total biomass. Other dominants included *L. xanthurus* (9.1% of the total biomass), *M. cephalus* (7.6%), *S. lanceolatus* (6.5%), *A. felis* (5.7%), *C. arenarius* (5.0%), *A. mitchilli* (3.7%), *S. plagiusa* (2.7%), *Pogonias cromis* (2.3%), *Lepisosteus oculatus* (2.0%), and *Dasyatis sabina* (2.0%). *Micropogonias undulatus* was the biomass dominant in 14 of 24 months (spring and summer), *M. cephalus* predominated in 5 winter months, *A. felis* in 4 fall months, and *S. lanceolatus* once in late summer. The monthly biomass patterns of *M. undulatus, M. cephalus, C. arenarius,* and *A. mitchilli* were significantly correlated between the two years of sampling (Table 10). *Anchoa mitchilli* was the only one of these four species that had a significantly higher annual biomass per tow (B/T) value in one of the two years. The monthly B/T values of *A. mitchilli* were higher in 11 of 12 months in 1963, significantly so in six of those months. Biomass catches were higher in the 1964 summer months for both *M. undulatus* and *C. arenarius* but did not affect the annual catch values. Monthly B/T differences occurred erratically in the *M. cephalus* population. Monthly biomass patterns were not correlated between years for *L. xanthurus, S. lanceolatus,* and *A. felis.* Catches of *L. xanthurus* were much higher in the

TABLE 8

Zone-subarea combinations of maximum mean number per tow (N/T) of 59 fishes collected in Galveston Bay, 1963–1964. Thirty-seven species are not included due to N/T values less than 0.1. Dashes indicate combinations wherein no species reached a maximum. Other information in Table 1.

Subarea	Channel	Open Water
GM	*Etropus crossotus* 1.2 *Centropristis philadelphica* 0.5	*Cynoscion arenarius* 22.3 *Prionotus tribulus* 1.4 *Porichthys plectrodon* 1.1 *Larimus fasciatus* 0.9 *Anchoa hepsetus* 0.6 *Cynoscion nothus* 0.5 *Prionotus scitulus* 0.1
TP	*Polydactylus octonemus* 10.3 *Peprilus burti* 0.4 *Astroscopus y-graecum* 0.2 *Lagodon rhomboides* 0.2	*Menticirrhus americanus* 4.4 *Orthopristis chrysoptera* 0.8 *Dasyatis sabina* 0.1
LG	*Stellifer lanceolatus* 116.4 *Bairdiella chrysoura* 0.8 *Gobionellus hastatus* 0.1	
UG	*Urophycis floridanus* 1.2 *Ancylopsetta quadrocellata* 0.1 *Opsanus beta* 0.1	*Anchoa mitchilli* 77.2
MS	*Symphurus plagiusa* 14.5 *Gobiesox strumosus* 0.6 *Chaetodipterus faber* 0.3 *Dorosoma petenense* 0.2 *Ophichthus gomesi* 0.2	-
TB	-	-
EB	-	-

Subarea	Shore	Peripheral
GM	-	-
TP	-	*Synodus foetens* 0.8 *Eucinostomus gula* 0.6 *Gobionellus boleosoma* 0.3
LG	*Oligoplites saurus* 0.4 *Chloroscombrus chrysurus* 0.1	*Achirus lineatus* 1.2 *Fundulus grandis* 0.1
UG	*Arius felis* 21.0 *Bagre marinus* 1.9 *Myrophis punctatus* 0.3	*Paralichthys lethostigma* 0.6 *Cynoscion nebulosus* 0.2 *Gobiosoma bosci* 0.1

TABLE 8 (Continued)

MS	*Sphoeroides parvus* 16.2 *Elops saurus* 0.1	–
TB	*Pogonias cromis* 0.1	*Lepisosteus oculatus* 0.3 *Trinectes maculatus* 0.3 *Dorosoma cepedianum* 0.2 *Ictalurus furcatus* 0.2 *Ictalurus punctatus* 0.1
EB	*Brevoortia patronus* 8.0	*Micropogonias undulatus* 235.2 *Leiostomus xanthurus* 54.4 *Mugil cephalus* 10.0 *Citharichthys spilopterus* 8.2 *Cyprinodon variegatus* 2.0 *Mugil curema* 1.0 *Menidia beryllina* 0.5 *Fundulus similis* 0.4 *Sciaenops ocellatus* 0.3

last seven months of 1964, which lead to a significantly higher biomass catch rate for that year, even though N/T values were similar. The difference in *S. lanceolatus* B/T values was again related to extremely high catches in August 1963. Although the annual B/T values for *A. felis* were similar, the variations between similar months in successive years led to a lack of correlation between 1963 and 1964. It was interesting to find, despite monthly variations, that the biomass catch rates for the total fish fauna were similar between years and that the monthly patterns were also correlated.

OTHER GALVESTON BAY STUDIES

Bechtel and Copeland (1970) conducted one year of quarterly fish sampling on 28 stations in the estuary, which included 8 stations in West Bay, an area not covered by the 1963–1964 survey. They used a 3-m trawl with 20-mm mesh wing and body and 6-mm mesh cod end towed for 10 minutes (day or night was not specified). In contrast, the 1963–1964 survey used a 3-m net with coarser mesh (35-mm body, 25-mm cod end) for 5-min daylight tows. Bechtel and Copeland were primarily interested in species diversity, and they concluded that pollution was responsible for reduced diversity in certain areas of the estuary. Few numerical data were presented, but several comparisons can be made: 1) *M. undulatus* and *A. mitchilli* were the most abundant species in both studies, 2) *L. xanthurus* and *S. lanceolatus* were more abundant in 1963–1964 than in 1969, while the reverse was true for *A. felis* and *C. arenarius*, and 3) numbers and biomass per tow were approximately three times higher in 1969 than in 1963–1964, probably due to the finer mesh net used in 1969.

There have been no other comprehensive studies of the fish fauna of the Galveston Bay estuarine system. Several investigations of environmental alterations have been made on limited portions of the estuary (Table 11);

TABLE 9

Monthly biomasses (grams, wet weight) of the 20 biomass dominants and of all species collected in Galveston Bay in 1963 and 1964.

	1963												
Species	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
Micropogonias undulatus	4875	7352	18648	53082	90409	52283	34950	19473	5943	3661	6773	5791	303240
Leiostomus xanthurus	3561	3004	4527	9958	6402	10276	8016	3810	2766	2766	1646	6781	63513
Mugil cephalus	8946	16947	3967	1659	1167	43	506	855	191	91	557	29904	64833
Stellifer lanceolatus	24	3	21	641	408	2236	5507	55773	3211	2705	1789	1108	73426
Arius felis	67	5	1625	2852	5444	4206	5016	11648	11263	8341	561	30	51058
Cynoscion arenarius	174	36	215	812	2551	5043	7808	6526	2946	2954	2936	2048	34049
Anchoa mitchilli	851	1759	1740	3442	5376	6374	1934	1928	2119	6234	5001	2481	39239
Symphurus plagiusa	832	1844	1460	874	848	1503	876	1455	1730	2493	3549	3987	21451
Pogonias cromis	2111	927	1030	631			1369	206	34	172	215	5379	12074
Lepisosteus oculatus				369			4499	9800					14668
Dasyatis sabina			5975	2721	2589	4891	1099	2761	233	485		475	21229
Menticirrhus americanus	747	1306	3029	766	714	842	245	245	1170	222	510	4861	14657
Sphoeroides parvus	273	6	479	342	441	1011	1785	2084	1838	782	1312	1802	12155
Brevoortia patronus	906	1764	2201	264	53	256	291	839	199	134	585	2897	9989
Archosargus probatocephalus	194	2933		1		1174	2564	2055		2463	1068		12452
Polydactylus octonemus			5	350	2661	3903	1842	747	294				9802
Paralichthys lethostigma	1899	2333	1183	893	1270	331	941	1287	879	106	557	361	12040
Bagre marinus					812	239	1763	3753	930	438			7935
Lepisosteus spatula												3178	3178
Citharichthys spilopterus	85	164	20	73	1239	1812	1755	1578	720	481	220	114	8261
Total Biomass, all fishes	29525	47041	49878	75822	127524	94297	96243	134968	40850	38197	31080	77093	842518
Total number of trawl tows	110	115	126	128	130	129	129	130	130	130	128	129	1514

	1964													2-YR
Species	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total	Total
Micropogonias undulatus	2168	4469	10995	26663	43777	39747	34983	14174	6004	2750	4988	6238	196956	500196
Leiostomus xanthurus	1311	2415	2319	1476	10251	9223	9990	8585	5038	3039	3663	3405	61437	124950
Mugil cephalus	14213	12255	698	1733	1185	929	222	809	206	1240	303	5789	39582	104415
Stellifer lanceolatus	64	100	52	329	415	1093	5282	1903	2448	1139	2747	530	16102	89528
Arius felis			2661	732	585	1720	4119	3830	3339	3700	5702	158	26546	77604
Cynoscion arenarius	15	69	43	151	2189	5570	11362	6625	2916	1716	1792	1375	33823	67872
Anchoa mitchilli	593	616	775	806	2249	517	522	189	313	2114	2660	618	11972	51211
Symphurus plagiusa	2818	1346	700	997	250	413	832	595	635	1077	1887	4030	15580	37031
Pogonias cromis	2177	2974			8443		457	233	134	242		4805	19465	31539
Lepisosteus oculatus		1362		5454	1304	786	4179						13805	27753
Dasyatis sabina			1942		669	1445		77	720		720	445	6018	27247
Menticirrhus americanus	312	1469	694	562	100	118	465	149	148	440	408	3132	7997	22654
Sphoeroides parvus	6	257	457	248	249	377	884	436	980	1078	1648	3384	10004	22159
Brevoortia patronus	676	1575	460	407	201	1128	195	701	770	200	670	1206	8589	18578
Archosargus probatocephalus	2526		322					791	1348	354			5341	17793
Polydactylus octonemus	43		5	268	3473	878	2436	237					7340	17142
Paralichthys lethostigma	993	496	11	55	339	611	483	83	71	53	436	737	4368	16408
Bagre marinus							213	3097	2259	261			5830	13756
Lepisosteus spatula					6804		1863						8667	11845
Citharichthys spilopterus			15	37	172	632	732	438	340	79	106	2	2553	10814
Total Biomass, all fishes	31338	31985	23745	42295	84043	68244	81887	44568	30327	21142	29424	38624	527622	1370140
Total number of trawl tows	128	128	65	65	65	65	65	65	65	65	65	64	905	2419

however, such studies are not truly inter-comparable with the 1963–1964 investigation due to variations in gear, numbers of stations, etc. Reid (1957) summarized trawl surveys of the East Bay subarea 6 months before and 6 and 18 months after the January 1955 opening of Rollover Pass (approximately 16 km northeast of Galveston, Figure 1). Reid associated year-to-year fluctuations in abundance and composition of the fish fauna with extreme changes in the salinity structure of East Bay due to the new pass. Reid found that *M. undulatus* and *A. mitchilli* were the subarea co-dominants (33.7 and 31.0% of the total fishes) in three successive Junes (1954–1956). In June of

TABLE 10

Comparison of monthly and yearly mean biomass (grams) of fishes per tow (B/T) collected over all stations for the seven biomass dominants and the total fish fauna in Galveston Bay, 1963–1964. Asterisk (*) indicates both significant differences ($\chi^2, P < .05$) between corresponding months in each year and significant correlations (r, $P < .05$) in trends between years.

	YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN-DEC	r
Micropogonias undulatus	1963	44.3*	63.9*	148.0	414.7	695.5	405.3	270.9	149.8	45.7	28.2	52.9	45.2	200.3	.925*
	1964	16.9	34.9	169.2	410.2	673.5	611.5*	538.2*	218.1*	92.4*	42.3	76.7*	97.5*	217.6	
Leiostomus xanthurus	1963	32.4*	26.1	35.9	77.8*	49.2	79.7	62.1	29.3	21.3	21.3	12.9	53.0	42.0	.342
	1964	10.2	18.9	35.7	22.7	157.7*	141.9*	153.7*	132.1*	77.5*	46.8*	56.4*	53.2	67.9*	
Mugil cephalus	1963	81.3	147.4*	31.5*	13.0	9.0	0.3	3.9	6.6	1.5	0.7	4.4	231.8*	42.8	.830*
	1964	111.0*	95.7	10.7	26.7*	18.2	14.3*	3.4	12.4	3.2	19.1*	4.7	90.5	43.7	
Stellifer lanceolatus	1963	0.2	0.1	0.2	5.0	3.1	17.3	42.7	428.0*	24.7	20.8	14.0	8.7	48.5*	.210
	1964	0.5	0.8	0.8	5.1	6.4	16.8	81.3*	29.3	37.7	17.5	42.3*	8.3	17.8	
Arius felis	1963	0.6	0.1	12.9	22.3	41.9*	32.6	38.9	89.6*	86.6*	64.2	4.4	0.2	33.7	.452
	1964	0.0	0.0	40.9*	11.3	9.0	26.5	63.4*	58.9	51.4	56.9	87.7*	2.5	29.3	
Cynoscion arenarius	1963	1.6	0.3	1.7	6.3	19.6	39.1	60.5	50.2	22.7	22.7	22.9	16.0	22.5	.962*
	1964	0.1	0.5	0.7	2.3	33.7	85.7*	174.8*	101.9*	44.9*	26.4	27.6	21.5	37.4	
Anchoa mitchilli	1963	7.7	15.3*	13.8	26.9*	41.4	49.4*	15.0	14.8*	16.3*	48.0	39.1	19.4*	25.9*	.707*
	1964	4.6	4.8	11.9	12.4	34.6	8.0	8.0	2.9	4.8	32.5	40.9	9.7	13.2	
Total Fishes	1963	268.4	409.1*	395.9	592.4	981.0	731.0	746.1	1038.2*	314.2	293.8	242.8	602.3	556.5	.782*
	1964	244.8	249.9	365.3	650.7	1293.0*	1049.9*	1259.8*	685.7	466.6*	325.3	452.7*	603.5	583.0	

TABLE 11

Comparison of species composition (as % of total fishes) and catch (numbers per tow, N/T) in the 1963–1964 Galveston Bay trawl survey with results of other trawl surveys in the estuary. Only stations on similar sites were compared. GB = this survey; R = Reid (1957); J = Johnson (1973); GS = Gallaway and Strawn (1974); H = Henningsen (1977). Other information in Table 1.

Sub-areas	Zones	Dates		# of Stations		# of Tows		Species	% of Catch		Mean N/T	
		R	GB	R	GB	R	GB		R	GB	R	GB
EB	0,S	6/54	6/63	Var.	13	171	39	*M. undulatus*	33.7	63.7	111.1	141.1
		6/55	6/64					*A. mitchilli*	31.0	16.9	102.2	37.2
		6/56						*L. xanthurus*	17.0	13.4	55.9	25.6
								B. patronus	5.7	0.6	18.8	1.2
								C. arenarius	3.7	2.3	12.2	7.4
								A. felis	1.3	0.2	4.3	0.4
								All fishes			322.9	218.5
									J	GB	J	GB
TB	0,S	J	GB	J	GB	J	GB	*A. mitchilli*	38.2	24.4	119.1	42.0
		1/70-12/71	1/63-12/64	13	12	718	444	*M. undulatus*	27.7	58.3	54.4	94.0
								B. patronus	18.7	1.1	16.5	2.2
								L. xanthurus	2.8	4.4	1.5	7.6
								A. felis	2.6	3.1	3.0	3.4
								C. arenarius	1.8	2.2	5.4	3.8
								All fishes			217.8	161.6
									GS	GB	GS	GB
UG	S	GS	GB	GS	GB	GS	GB	*M. undulatus*	41.6	34.8	152.2	38.1
		1/68-12/69	1/63-12/64	11	2	257	75	*A. mitchilli*	29.1	25.8	106.5	28.2
								A. felis	15.6	19.2	57.3	21.0
								B. patronus	5.2	1.0	19.1	1.1
								P. octonemus	3.9	0.4	14.4	0.4
								C. arenarius	1.3	1.8	4.9	1.9
								L. xanthurus	1.1	0.6	4.0	7.2
								All fishes			366.2	109.6
									H	GB	H	GB
GM	C,O	H	GB	H	GB	H	GB	*M. undulatus*	64.7	19.2	126.7	15.2
		5/75-5/76	1/63-12/64	2	2	52	75	*Symphurus* spp.	11.2	7.7	21.9	6.1
								S. lanceolatus	8.9	22.9	17.3	18.1
								P. octonemus	8.0	2.8	15.6	2.2
								C. arenarius	2.4	22.7	4.8	17.9
								A. mitchilli	1.2	9.2	2.4	7.2
								All fishes			195.9	78.9

1963 and 1964, *M. undulatus* was relatively more abundant (63.7% of the fishes) and *A. mitchilli* was relatively less so (16.9%). Reid found higher catch rates for the total fish fauna and for all dominant fishes except *M. undulatus* than did the 1963–1964 survey. One of the factors that could have influenced the differing catches was sampling gear. Reid used several nets; included were a 3-m trawl with a 45-mm mesh body and either a 25-mm or a 10-mm mesh cod end and a 4.6-m net with a 38-mm mesh body and cod end or a 10-mm mesh cod end. Trawl-hauls were either of 10- or 30-min duration or 1 mile in length. In contrast, the 1963–1964 survey employed only a 3-m net with a 35-mm mesh body and 25-mm cod end towed for 5 minutes.

Johnson (1973) summarized surveys conducted from October 1969 through December 1971 that centered around the start-up of the Cedar Bayou power generating station in the San Jacinto River and Trinity Bay subareas (approximately 20 km northwest of Galveston). Compared with the 1963–1964 study, Johnson found relatively more *A. mitchilli* and *B. patronus* and relatively fewer *M. undulatus* on stations not impacted by the power plant. However, there were several differences in sampling methods which may have influenced catches. Johnson had more shore zone and fewer open water zone stations (10 and 3, respectively) than did the 1963–64 study (6 of each), and all of Johnson's shore stations centered on the effluent site while the earlier study sites fringed the whole subarea. Johnson also sampled only at night, employed a 5-mm mesh cod end, and sampled twice monthly for the complete period. The present survey was conducted during daylight, employed a net with a 25-mm cod end, and switched from twice monthly to monthly sampling after 14 months. Another factor that influenced catches was the existence in Johnson's survey of a warm-water plume (which attracted fishes and which did not exist earlier).

Gallaway and Strawn (1974) also studied the fishes near a power station discharge canal in the Upper Galveston Bay subarea, approximately 14 km west-northwest of Galveston, which began operating in 1966. Their trawl survey was conducted from January 1968 through December 1969 and, though they used a larger trawl (6.1-m) with a smaller mesh cod end (5-mm mesh liner) and sampled nine more stations only at night, their results were quite similar to those of the earlier survey (Table 11). In both studies, *M. undulatus* was the dominant fish and together with *A. mitchilli* and *A. felis* comprised over 75% of the fish catch in the Upper Galveston Bay shore zone. However, catch rates for the total fish fauna were three times higher in the later study and were 2–20 times higher for all major species (except *L. xanthurus* whose catch rate was slightly higher in the earlier study).

Henningsen (1977) conducted a trawl survey off the mouth of the Bolivar Roads Tidal Pass from May 1975 through May 1976. The fish fauna were quite dissimilar to that found in 1963–1964, both in the channel and open water zones, despite the use of a similar net and daytime sampling (Table 11). Henningsen found that *M. undulatus* comprised over 60% of the fishes in both areas. The 1963–1964 investigation found that only 18–20% of the catch was *M. undulatus* and that *S. lanceolatus, C. arenarius,* and *A. mitchilli*

were relatively more abundant. Henningsen's overall catch rate was also 2.5 times that of the earlier survey.

The general lack of agreement on species composition and abundance between successive studies of the Galveston Bay estuary is in part due to different sampling methodologies. Other potential factors include short- and long-term fluctuations in actual species abundance linked to environmental fluctuations. For example, long-term studies of the Apalachicola estuary of northwest Florida have indicated that fluctuations in fish population sizes and species compositions may be linked to preceding or concurrent fluctuations in pollutants, local rainfall, river discharge, salinity, and temperature (Kobylinski and Sheridan 1979; Livingston 1977; Livingston *et al.* 1976). Such cycles can be seasonal, yearly, or even longer (5–7 years, Meeter *et al.* 1979). However, the possibility exists that, even with annual and areal variations in species composition and numerical catch rates, there may be a stable level of fish biomass supported by the estuary.

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TIME COURSE OF OSMOTIC ADAPTATION WITH RESPECT TO BLOOD SERUM OSMOLALITY AND OXYGEN UPTAKE IN THE EURYHALINE TELEOST, *SCIAENOPS OCELLATUS* (RED DRUM)[1]

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ABSTRACT

Blood serum osmolalities of juvenile red drum, acclimatized at 24°C and 30 ppt salinity and abruptly transferred to separate salinities of 40, 30, 20, 10 and 2 ppt, became stabilized at these new levels after 24 hours. Variability at the 40 and 2 ppt salinity levels was greater than at intermediate levels. Isotonicity was at about 11 ppt (320 m0sm kg^{-1}). There was little change in hematocrit values over the various salinity changes or time intervals. There was no indication that selective mortality removed individuals with excessive osmotic stress response.

Standard metabolic rates at 28°C, as measured by oxygen uptake rates 24–48 hours after salinity acclimated fish had been abruptly exposed to salinity increases or decreases of 10 ppt or less between 50 and 1 ppt, tended to be restabilized; up to 24 hours the greatest metabolic variability was at the highest (50 ppt) and lowest (1 ppt) salinities. Metabolic rates were minimal at 20 ppt and about 24 and 37% higher at the 50 and 1 ppt salinity extremes, respectively. The increased metabolic rates for the red drum at these extremes are smaller than for several other local euryhaline species. Explanations for departures from the U-shaped standard metabolism-salinity curve at lowest salinities could involve either shifts to relatively lower cost physiological processes or population shifts by selective survival of individuals having the lowest energy requirements. However, at both salinity extremes the rapid 24- to 48-hour stabilization of both serum osmolalities and standard metabolic costs indicates that this species is well adapted to natural rapid salinity changes.

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INTRODUCTION

Coastal and estuarine fishes often encounter fluctuations in salinity due to variations in rainfall, freshwater inflow, evaporation, and seawater tidal inflows. Increases in freshwater impoundments and various human ac-

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tivities have resulted in decreases in freshwater inflow regimes (but possibly with exacerbated flood conditions) in recent years. The general result of human activity is for increased salinities in coastal waters where adverse effects on biota might be expected. In south Texas coastal waters, the most obvious adverse effects are those of hypersalinity resulting from prolonged drought or of sudden freshening during and immediately following very heavy hurricane rains. Important considerations in the management of coastal fisheries thus involve knowledge of salinity effects and rates of adaptation to salinity changes. From a more theoretical point of view, adaptation and selection among organisms subject to stresses can be interpreted only if variable-environment and species compatibility influences can be distinguished (Schoener 1982).

The effects of salinity on oxygen consumption responses of euryhaline fishes have been reported by many investigators. In certain species, physiological stresses associated with ambient salinity appear to be minimized when ambient salinity is isosmotic with the blood (Kinne 1964, Rao 1968, Rao 1971, Farmer and Beamish 1969, Nordlie and Leffler 1975). In other species, metabolic responses of *Gillichthys mirabilis* (Courtois 1976), *Ambassis interrupta* (Nordlie 1978), and *Cynoscion nebulosus* (Wohlschlag and Wakeman 1978), are optimal at salinities considerably different from isosmotic points.

Although salinity can have significant effects on energy budgets (Brett 1970, Brett and Groves 1979) and on activity (Wohlschlag 1981), rates of adaptation and short-term impacts of salinity fluctuations are not widely known. In the present study, the time course of adaptation of the coastal red drum, *Sciaenops ocellatus,* to abrupt salinity changes was evaluated in terms of changes in blood serum osmolality and standard oxygen consumption rates.

MATERIALS AND METHODS

BLOOD SERUM OSMOLALITY

Hatchery-reared juvenile red drum that ranged from 1.1 to 3.8 g were obtained from The University of Texas Mariculture Laboratory at Port Aransas, Texas. These fish were held in a 1.8 m diameter circular holding tank in filtered sea water at 30 ppt salinity and 24°C for at least 7 days. During this acclimation period they were fed chopped shrimp daily.

Following acclimation, randomly selected groups of 7 each were transferred from the acclimation tank to 5 separate aquaria at respective salinities of 40, 30, 20, 10 and 2 ppt. At time intervals of 1, 4, 8, 12, 24, 36, and 48 hours after these transfers, one fish at a time was removed from each aquarium for serum osmolality determination. The experimental procedure was repeated so that a total of 70 individual serum osmolality determinations was made.

To obtain blood samples, each fish was first blotted dry and its caudal peduncle then severed with a scalpel. Blood from the caudal artery was immediately taken into a heparinized capillary tube and centrifuged for the determination of the hematocrit. An 8-μl sample of plasma from the capillary tube was then placed into a vapor pressure osmometer (Wescor® 5100C) for measurement of osmolality.

OXYGEN UPTAKE RATES

Red drum that ranged from 72.8 to 196.5 g were collected from an estuarine pass near Port Aransas, Texas during July at ambient salinities near 30 ppt and temperatures from 28 to 31°C.

During recovery from the effects of capture, the fish were held in large circular holding tanks through which laboratory seawater from the Aransas Pass Ship Channel at ambient temperatures and salinities was continuously pumped for at least a 7-day period. Fish were then selected in groups of 3 each and acclimated with fasting at 28°C and initial experimental salinities for 48 hours prior to respiration determinations.

The respiration apparatus consisted of a bank of 4 cylindrical transparent acrylic plastic flow-through chambers, which had a common aerated water source. The bank of chambers was immersed in a large temperature- and salinity-controlled aquarium as described by Vetter (1982) and Wohlschlag and Parker (1981). The inside diameter of the chambers was small enough (14 cm) so that the red drum tended not to turn during their confinement; they usually remained quietly on the chamber floor during the entire experimental period. Oxygen consumption rates within the chambers were calculated from the difference between the oxygen contents of the inflowing and outflowing water as determined with an oxygen electrode (Radiometer Model E-5046 with a PHM 71 electrode equipped with an acid-base analyzer) and the measured flow rate of water through each chamber. Oxygen content of the water entering each chamber was always near saturation, and flow rates were adjusted so that the P_{O_2} was usually reduced by 10–15 mm Hg in the outflowing water.

Three of the respiration chambers were used for acclimated fish; the fourth was used as a control to determine any oxygen consumption not attributable to fish so that oxygen consumption rates of the fish in the other chambers could be adjusted accordingly. The chambers were covered with black plastic sheeting to minimize visual stimuli, while the entire aquarium was enclosed by black curtains. The fish were allowed to remain in this stimulus-reduced condition for 12 hours before any respiration rate determinations were made. Immediately after the initial determination of the oxygen consumption rates in the chambers, the salinity of the water flowing through the chambers was changed. Oxygen consumption rates were again monitored at intervals of 1, 4, 8, 12, 24, 32, 36, and 48 hours after the salinity change.

The salinity changes were made either by the addition of deionized water or of prepared sea salts in increments of 10 ppt in the range between 10–50 ppt, while smaller increments were used below 10 ppt.

RESULTS

BLOOD SERUM OSMOLALITY

Blood serum osmolality pairs of values at the various time intervals following abrupt changes in salinity are tabulated (Table 1) to show both trends and the degree of variability in the ranges of the paired measurements. The time course of the trends for these juveniles are illustrated in Fig. 1 where mean osmolality values are plotted against elapsed time for each of the treatments. Generally the greatest variability occurs within 4–12 hours following salinity changes, while stabilization begins after about 24 hours. Final serum osmolalities determined 48 hours after the salinity changes indicated an approximately linear relationship between blood serum osmolality and ambient salinity over the range of salinities studied (Fig. 2). Blood serum was isotonic with ambient water at about 320 m0sm kg^{-1}, or 11 ppt.

Hematocrit values for the red drum in this study ranged from 21–28% with most values close to 24%. No correlations were found between hematocrit and ambient salinity or blood serum osmolality.

TABLE 1

Forty-eight-hour time course of blood serum osmolality levels (mOsm kg^{-1}) for duplicate experiments on red drum subjected to abrupt changes in ambient salinity levels.

Salinity Change (ppt)	Elapsed Time in Hours						
	1	4	8	12	24	36	48
30 - 40	352	365	396	382	358	345	--[1]
	361	372	380	376	355	357	360
30 - 20	344	340	329	335	331	318	336
	336	337	335	326	333	330	323
30 - 10	330	315	322	318	325	322	314
	328	325	308	315	318	316	325
30 - 2	320	306	310	295	318	325	310
	316	318	291	308	298	309	314
Control:							
30 - 30	340	334	337	348	343	350	339
	347	342	345	341	351	344	346

[1]No value recorded due to death of fish.

OXYGEN UPTAKE RATES

Oxygen consumption rates in mg O_2 kg^{-1} hr^{-1} following rapid salinity changes for the red drum at 28°C are shown in Fig. 3. Note that the separate pairs of plots in Fig. 3 are based on both decreasing and increasing salinities. Although the oxygen consumption rates were highly variable and erratic for approximately the first 24 hours after the abrupt salinity change, the rates tended to become stabilized after about 24 hours. Whether the salinity increased or decreased, there was a tendency for the final 24- to 48-hr averages at a given salinity to be about equal and there was no pronounced tendency for the standard deviations to vary with the salinity levels (Fig. 3). The stabilized rates when averaged at each ambient salinity, however, increased with salinity levels above and below 20 ppt as indicated in Fig. 4.

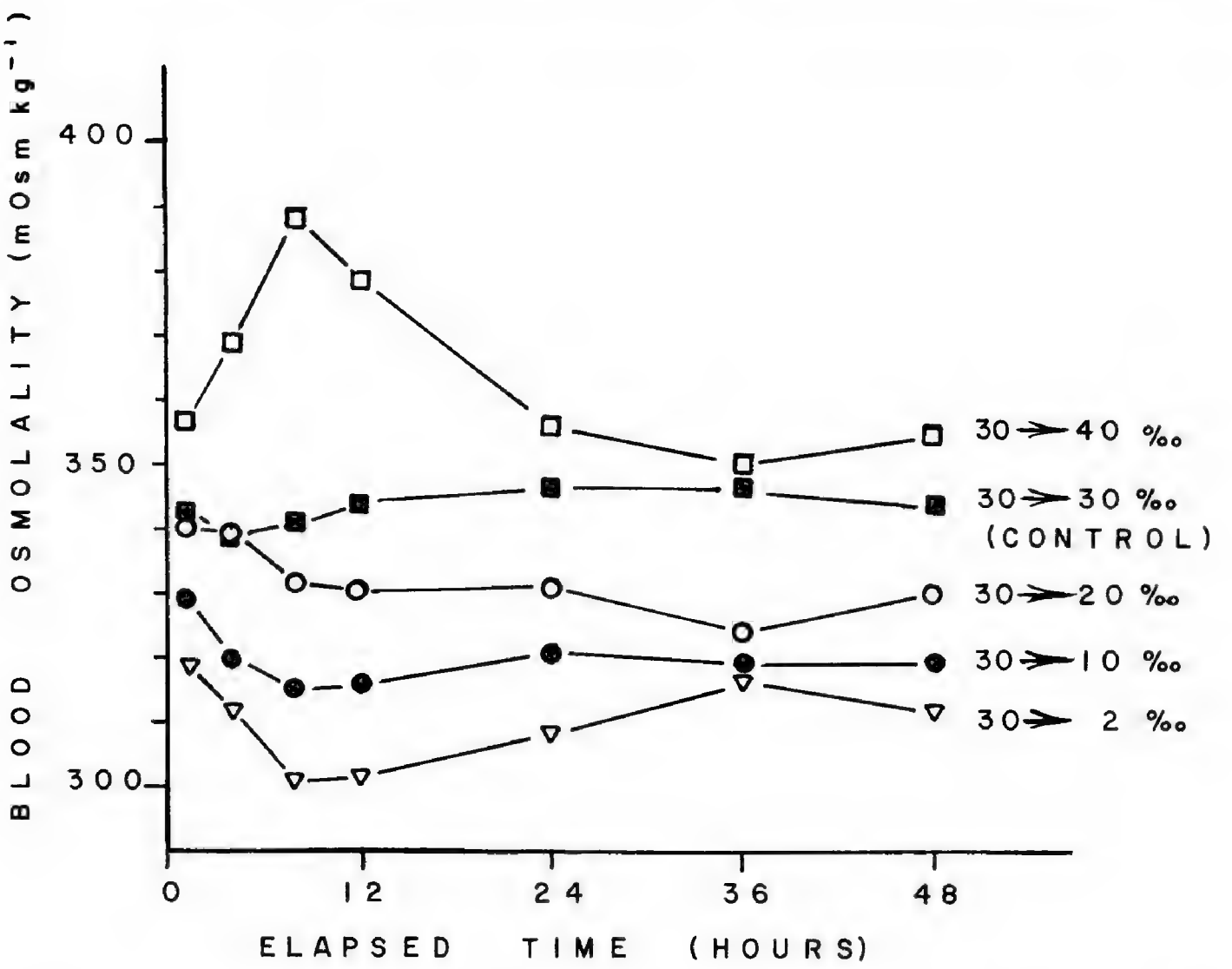

FIG. 1. Mean blood serum osmolality levels (m0sm kg^{-1}) of red drum transferred from 30 ppt salinity to salinities of 40, 30, 20, 10, and 2 ppt after successive time intervals of 1, 4, 8, 12, 24, 36, and 48 hours.

DISCUSSION

BLOOD CHARACTERISTICS AND SALINITY

In nature *Sciaenops ocellatus* is a broadly euryhaline species. After hatching in late summer and fall along coastal seawaters, the young immediately migrate to adjacent estuaries; by the end of winter and through spring and summer of their first year, the rapidly growing young are exposed to a wide range of salinities over the diverse coastal and estuarine habitats (Gunter 1945, Simmons and Breuer 1962, Perret *et al.* 1980, among others). The general physiological aspects of the various osmoregulatory processes that may be involved over such salinity ranges are reasonably well known, as indicated by the review of Maetz (1974). However, the general ecological and evolutionary significance of the relative rapidity with which this and similar species adjust to broad salinity changes is more abstruse, even though the results of Table 1 and Figs. 1 and 2 indicate excellent agreement with what probably occurs in wild fish.

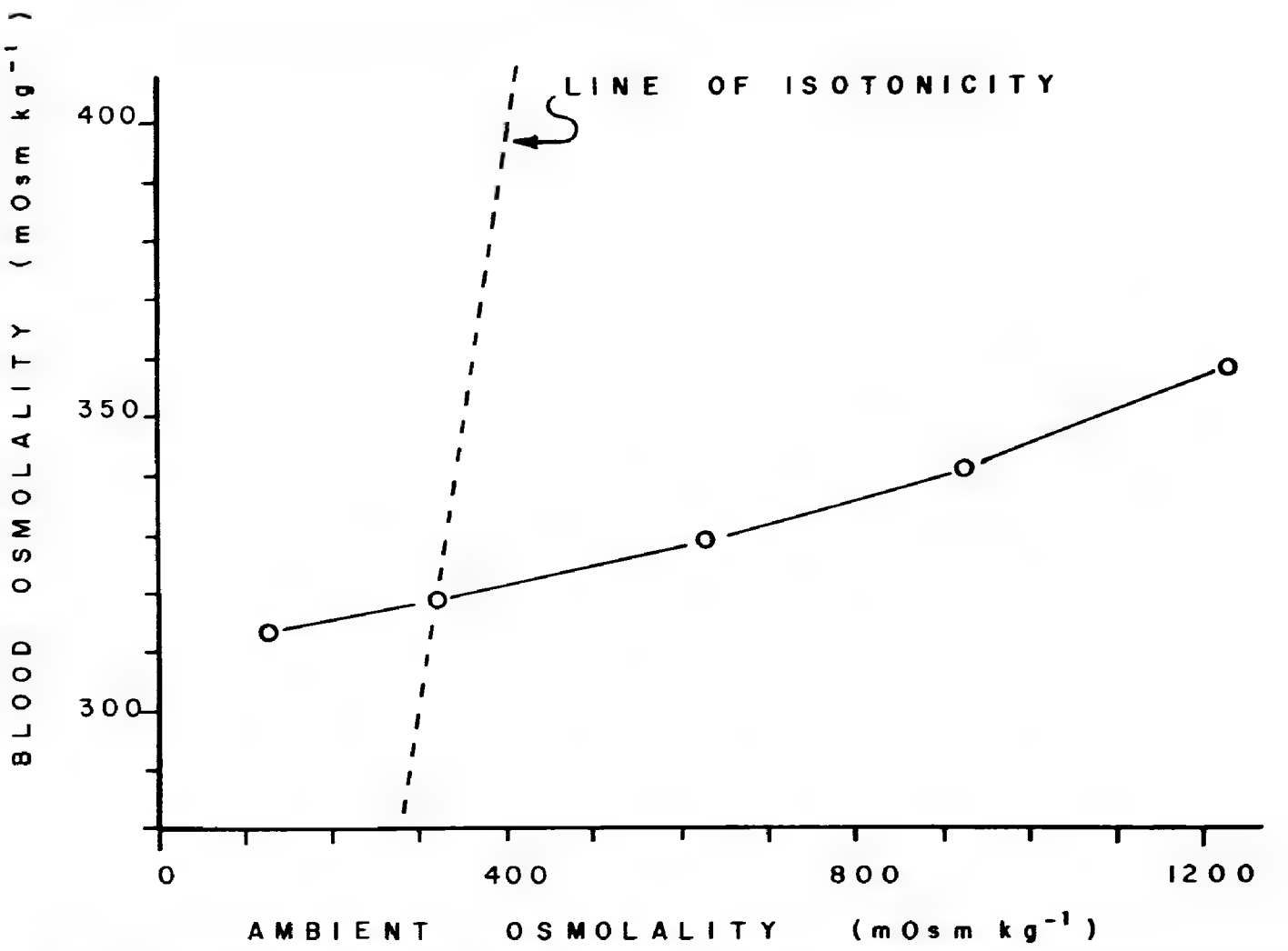

FIG. 2. Plot of blood serum osmolality levels (m0sm kg^{-1}) of juvenile red drum 48 hours after transfer to various salinities and comparison to line of isotonicity.

The ability for rapid adjustments to new salinities is of obvious advantage to most estuarine organisms. The approximate 24 hours required for blood serum osmolalities of the juvenile red drum to reach a new steady state following abrupt changes from 30 ppt salinity to a range of 2 to 40 ppt is an intermediate time. Parry (1966) reported 36 hours for juvenile chum salmon and about 12 hours for flounder were required for adjustment to comparable salinity changes. Similar periods have also been reported for other estuarine species (Schmidt-Nielsen 1977, Barton 1979). How stable the adjustments are and whether they are true measures of long-term (evolutionary) adaptation need further confirmation.

Some insight into the adjustment time and the serum osmolality levels that accompany abrupt ambient salinity changes are evident from Table 1 and Fig. 1 which indicate increased variability in blood osmolality was associated with salinity changes from 30 to 2 ppt and from 30 to 40 ppt. From other unpublished research with small red drum, this pattern seems to prevail above and below a 20 to 30 ppt acclimation range. Michael Gunter (1979, unpublished MA thesis, University of Texas) indicated that blood serum osmolality values for 1- to 5-g red drum tended to become bimodal within a few hours after salinity increases; in these cases the fish with the highest values tended to die off and thus reduce variability in osmolality about the various averages after 48 hours.

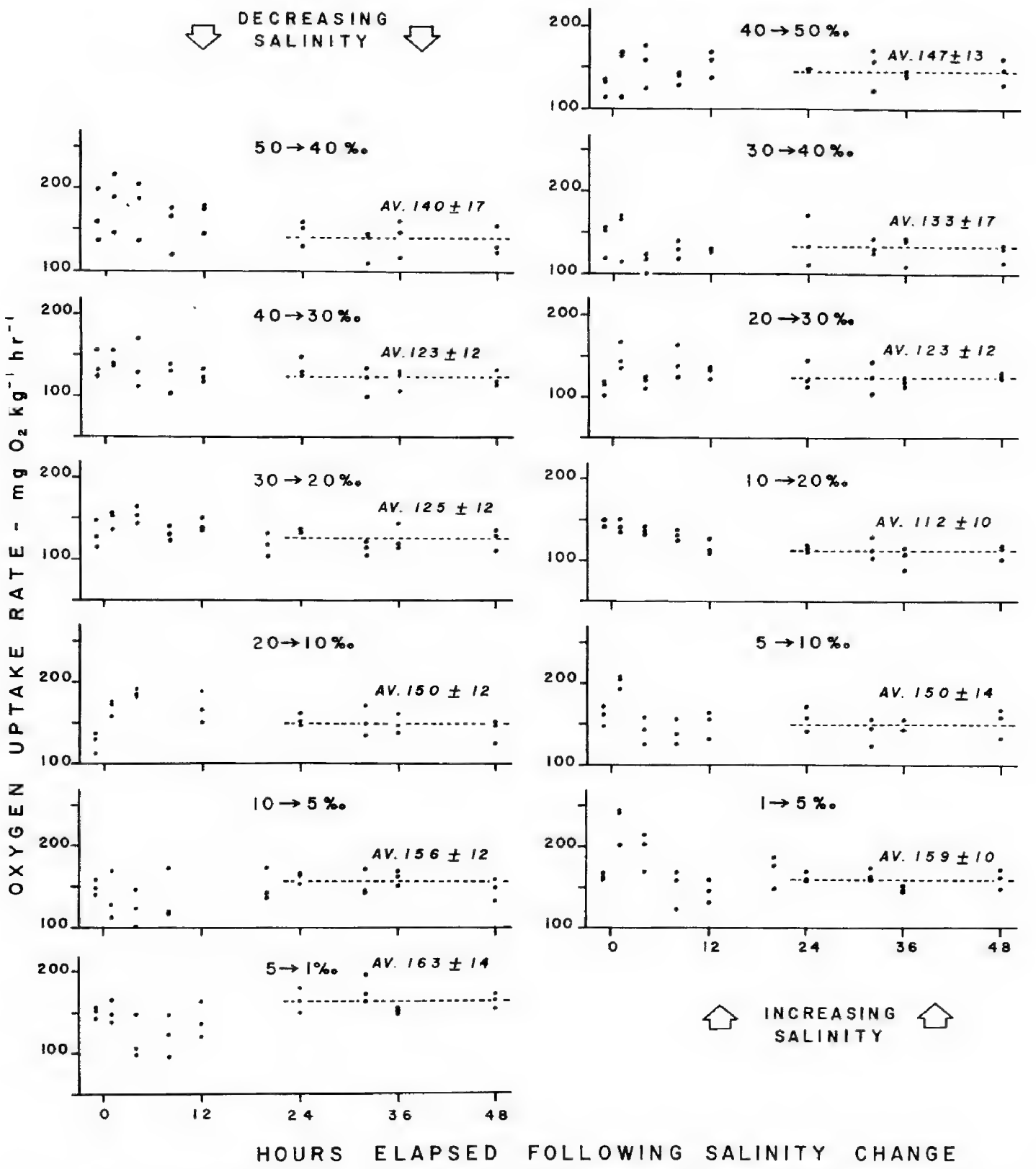

FIG. 3. Triplicate oxygen consumption rate determinations (mg O_2 kg^{-1} hr^{-1}) of quiescent, fasted subadult to adult red drum following abrupt salinity changes, indicated separately for each plot. Means ± standard deviation at the 24- to 48-hour intervals are indicated by dashed line for each plot. Initial triplicate determinations are slightly before zero time.

The differences between observed serum osmolalities and isotonicity in Fig. 2 indicate the degree to which the juvenile red drum are imperfect osmoregulators. However, there is the possibility that relatively large natural salinity changes would induce selected mortality whose ultimate effects would be to reduce the discrepancy from the 48-hour laboratory results and isotonicity shown in Fig. 2. In any case, the osmotic differences between serum and environmental salinities are considerably above and below the

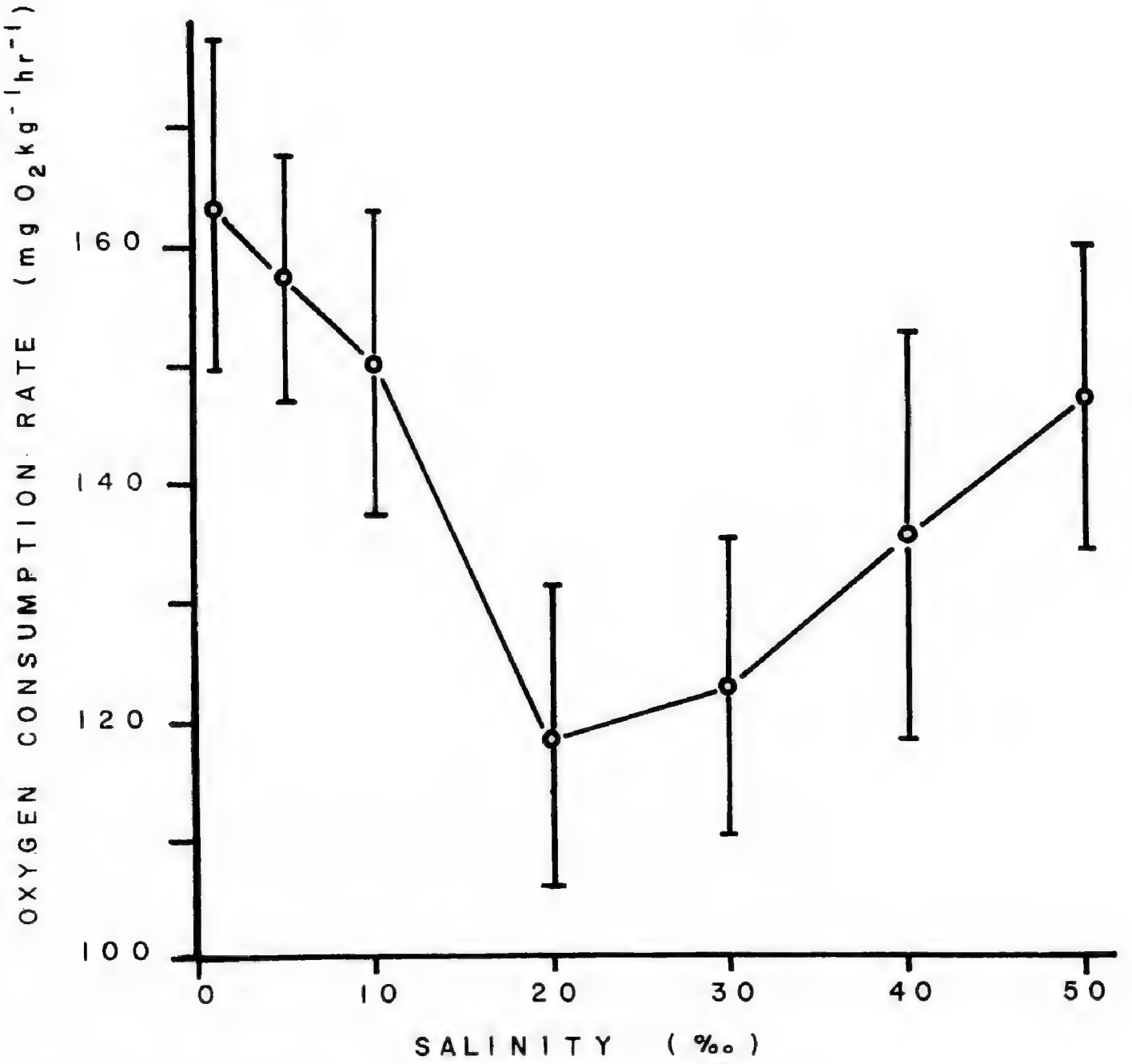

FIG. 4. Mean stabilized oxygen consumption rates (mg O_2 kg^{-1} hr^{-1}) ± standard deviation of red drum at various salinities.

320 m0sm kg^{-1} isosmotic point in Fig. 2. There is no evidence that any unusual physiological mechanisms are involved in the adjustments by red drum to ambient south Texas coastal salinities, which are ordinarily higher than 320 m0sm kg^{-1} (about 11 ppt salinity) south from San Antonio Bay to the Mexican Laguna Madre. Certainly major red blood cell volume changes are not involved.

The fact that there was little response or response variability in packed blood cell volume (hematocrit) at different salinities probably indicates that salinity stress within the ranges studied is subjected to normal "tolerance" physiological processes, rather than "resistance" processes or stress, which would imply an increase in hematocrit values (Swift 1982).

SIZE DIFFERENCES

Energy costs of osmoregulation have been estimated for many euryhaline teleosts (Kinne 1964, Farmer and Beamish 1969, Rao 1971, Nordlie and Leffler 1975). Such costs vary among species and often appear to be influenced by variables such as weight and temperature (Parry 1966, Kinne 1967, Fry 1971, among others). The red drum osmolality and standard metabolic responses to different salinity levels in this study were apparently little affected by their weight.

The smaller size of the red drum in the osmolality experiments and the larger size in the standard (maintenance) metabolism experiments discussed below would appear to be distinguishable only as response time biases to the salinity changes. Over a weight range of 1.0 to 147.5 g, Gunter (1979) showed that the effects of salinity changes were a more immediate response and adjustment by the smaller fish, but after about 30 hours, the "recovery stabilization" level was the same for all sizes. Laboratory studies of effects of salinity on osmolality and standard metabolism for the very large drum, two orders heavier (10 kg or more) do not exist; interpretation of their possible environmental preferences along coastal areas with relatively high salinities and with less erratic fluctuations is not very definitive at this time.

Another size-related involvement was from the use of small hatchery fish during the late spring and summer, when wild fish that have hatched the previous autumn exceeded the useful size range for the experiments. The hatchery cultured fish could be artificially induced to spawn most of the year. The fish used were about 9 months old and had been variously subjected to conventional treatments by malachite green, formaldehyde, a freshwater regimen, and antibiotics for a series of infections. The possible selective effects of these treatments could have selected survivors differentially for the osmolality or standard metabolic rate experiments, but the only evidence of differences from preliminary studies between hatchery and wild fish appeared to be small and to be related to differences in condition (fatness), active metabolic rates, and swimming rates.

RESPIRATORY METABOLISM AND SALINITY

Oxygen uptake rates (after stabilization) in this study were considered to be equivalent to the standard metabolic rates of the quiescent, fasted *Sciaenops ocellatus* reported in Wohlschlag (1981). The red drum standard oxygen uptake rate responses to ambient salinities have a U-shaped relationship (Fig. 4) similar to the metabolic responses reported for other estuarine fishes (Remane and Schlieper 1971, Nordlie 1978, Wohlschlag and Wakeman 1978). Of the four general patterns of metabolic responses categorized by Nordlie (1978), the red drum showed Nordlie's response "Pattern III" in which the rate of standard oxygen consumption is minimal at an intermediate optimal salinity that is not isosmotic with the blood serum.

As might be expected, after abrupt salinity changes and before stabilization, the amount of metabolic variability and the pattern of variability depends on the salinity level of initial acclimation and whether the abrupt salinity change is upward or downward. From the scatter plots of Fig. 3, it would appear that the initial scatter is greatest at the highest and lowest salinities; a similar scatter pattern of the osmolality data (Table 1, Fig. 1) corresponds to the same extreme salinity ranges. Further studies of this type of variation at environmental extremes should be useful in explaining processes of adaptation and selection.

Following stabilization of the oxygen uptake rates after 24 hours, it is apparent that the average rates have relatively low standard deviations (Figs. 3 and 4), except possibly at some of the higher salinities. This type of consistency was also evident from *Cynoscion nebulosus* measurements (Wohlschlag and Wakeman 1978).

A number of studies have failed to show appreciable increases in oxygen consumption rates of salt-transporting tissues of euryhaline fishes with changes in ambient salinity (Lotan 1966; Holmes and Stott 1980; Leray, Colin, and Florentz 1981). Marked changes in oxygen consumption rates of such fishes are probably related more to altered intra- and inter-cellular environments than to energetic demands of osmoregulation *per se* (Potts 1954, Nordlie 1978).

Among a list of factors influencing oxygen consumption, Brett (1970) reported that the effects of salinity are often relatively small compared with other factors, and commonly result in variations of only 10–15% in the standard metabolic rate. However, the standard rates of the mullet, *Mugil cephalus,* about doubled as ambient salinity increased from 100 to 1600 m0sm kg^{-1} (4–58 ppt salinity) according to Nordlie and Leffler (1975). Wohlschlag and Wakeman (1978) reported an approximate doubling of the spotted seatrout, *Cynoscion nebulosus,* standard metabolic rate as the salinity decreased to 10 ppt or increased to 45 ppt from a metabolic minimum at about 20 ppt. In this study, the red drum, *Sciaenops ocellatus,* standard rate increased about 24–37% at salinity extremes, compared to the optimal rate at 20 ppt as shown in Fig. 4. Thus over the range of salinities investigated, the red drum seems to require relatively less energy to accommodate to salinity extremes than either the mullet or the spotted seatrout . Whether such energy requirements for maintenance (standard metabolism) at other than intermediate estuarine salinities have any additional significant effects on foraging (swimming) activity, assimilation, growth, and general well-being of the red drum are the subjects of continuing studies.

One of the essential future studies will be to determine the meaning of the normal (and natural) variability of generalized functions, such as respiratory metabolism, for surviving populations at or near environmental stress levels where two extreme alternative interpretations are possible: (1) New adaptational functions and processes can become dominant and the population can be adapted to the new environmental conditions with ordinary

response variability; or (2) There can be selective mortality that involves survival of individual members with differential selection among existing adaptational functions and processes.

Of special interest is the fact that the shape of the left limb of the Fig. 4 indicates a somewhat diminished rate of increase in metabolic cost as salinity diminishes. In the case of the red drum, their propensities for acclimation to freshwater reservoirs is well known (Lasswell *et al.* 1978). The shape of the corresponding curve for the spotted seatrout, *Cynoscion nebulosus,* indicates an accelerated rate of metabolic increase with decreasing salinity and a general inability to adjust readily to freshwater environments (Wohlschlag and Wakeman 1978). The shape of metabolic compensation curves with respect to salinities also helps explain interspecific and size-specific differences among these and other sciaenids (Wohlschlag 1981); seasonal metabolic compensation curves with respect to temperature also indicate the degree of estuarine adaptation for sympatric seatrout species (Vetter 1982).

Although the acclimation times of this study indicated stability at the upper salinity levels for the oxygen uptake rates and for osmolality, it is speculative whether or not these physiological characteristics could be changed with longer acclimation times to the higher salinities. At higher salinities, any acclimation system that would reduce metabolic maintenance costs to levels nearer to those at the optimum (about 20 ppt) level would have considerable adaptive significance in south Texas and other estuarine areas that tend toward hypersalinity.

The adaptational importance of the salinity level to the metabolic energy for maintenance thus is emphasized by the shape and displacement of curves like that of Fig. 4. The relationships of this type of data to general physiological energetics are well understood, particularly from laboratory and hatchery data (Brett and Groves 1979), but there are relatively little new data on how environmental changes in salinity *regimes* might predict whether or not a fish species would survive naturally in a given locality. Also, as discussed by Schoener (1982), interspecific competition versus variable-environment controversies might better be reconciled if more empirical physiological energetics data could be directly related to natural or induced changes in the environment.

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ABUNDANCE OF BOTTLENOSE DOLPHINS IN CORPUS CHRISTI BAY AND COASTAL SOUTHERN TEXAS

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ABSTRACT

Aerial survey sightings were used to estimate the number of bottlenose dolphins *(Tursiops truncatus)* present in coastal waters between Aransas Pass and Brownsville, Texas, from 21 to 30 September 1979. Using line-transect methods, the populations in Corpus Christi Bay and in the coastal Gulf of Mexico were estimated, with 95% confidence limits, as 103.4 (67.3, 139.5) and 300.5 (226.6, 374.4), respectively. Average counts of dolphins actually observed in the major passes were 29.3 (Aransas), 17.7 (Mansfield), and 32.4 (Brazos Santiago). Shore observers stationed at the three passes provided data concerning herd size and numbers of dolphins present that were in good agreement with the aerial data. The total population in the study area at the time of the surveys was estimated as 373 to 593. Calves comprised 6.3–6.9% of all animals observed from the aircraft. In general, the dolphins were concentrated in or near the passes and dredged ship channels. Only three sightings were made in Laguna Madre proper. Feeding was observed in association with shrimp boats and in or along the edges of mud boils, tide rips, and surf lines.

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INTRODUCTION

From 21 to 30 September 1979, we conducted low-altitude aerial surveys of inland and coastal marine waters of Texas between Aransas Pass (approx. lat. 27°24′N, long. 97°01′W) and Brazos Santiago Pass (approx. lat. 26°04′N, long. 97°09′W), including Corpus Christi Bay and Nueces Bay, the Laguna Madre complex, and coastal waters inside the 18-m contour. The purpose of the study was to assess distribution, density, and relative age composition of the local bottlenose dolphin *(Tursiops truncatus)* population, and to develop standard survey procedures that could be used by the National Marine Fisheries Service in fulfilling its monitoring and management responsibilities under the Marine Mammal Protection Act of 1972 (Leatherwood and Show 1980, Leatherwood and Reeves 1982).

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DESCRIPTION OF THE STUDY AREA

Laguna Madre is the only major hypersaline lagoon in the semi-arid region of the United States, forming a nearly continuous, 350-km long system with Laguna Tamaulipas of northern Mexico. Detailed descriptions of hydrography (Collier and Hedgpeth 1950; Behrens 1966; Smith 1978) and biology (Hellier 1962; Breuer 1957, 1962; Simmons 1957; Hedgpeth 1947, 1967) of Laguna Madre are available. Prior to 1948 there were, in effect, two lagoons, one (Upper Laguna Madre) extending from Corpus Christi Bay south to Baffin Bay, and the other (Lower Laguna Madre) from Baffin Bay south to the Rio Grande River. The two were separated by a broad salt flat, with sand and mud substrate, which was inundated only infrequently during periods of strong winds and storm swells. In 1948 an Intracoastal Waterway (ICW) was completed between Corpus Christi Bay and Port Isabel; it provided a dredged channel 3.6 m deep and 37.5 m wide through the entire length of the Laguna.

In addition to the ICW, three major dredging projects have changed the configuration of the Laguna's bottom since 1948. There is now a 25-km ship channel joining Brazos Santiago Pass and the port of Brownsville. It is 10.8 m deep and 30–300 m wide. A cut was made through Padre Island at Port Mansfield. This artificial pass is connected to the mainland by an 8 km channel, 3.6 m deep and 30 m wide. Also, 35 km of Arroyo Colorado has been dredged to open Port Harlingen with a channel 2.7 m deep and 37.5 m wide.

Corpus Christi Bay is the embayed mouth of the Nueces River. It is shallow, with a maximum depth at mean low water of 4.6 m and an average depth of 2.8 m (Collier and Hedgpeth 1950). Its bottom contour has been likened to a frying pan, "falling off abruptly from the shores to a more or less uniform depth of twelve feet" (Collier and Hedgpeth 1950). Tidal amplitude in the bay is less than 0.3 m.

Off southern Texas, the Gulf of Mexico forms a broad, shallow, largely sand-bottomed shelf. Depths of 200 m and 2,000 m are not reached until 75–100 km and 160–200 km offshore, respectively.

BOTTLENOSE DOLPHINS

The most common cetacean species in Texas coastal waters is the bottlenose dolphin (Schmidly and Melcher 1974, Schmidly and Shane 1978). Here, as in other parts of the Gulf of Mexico, these dolphins are distributed from shallow riverine and estuarine habitat, including bays, lagoons, and the ICW, into the Gulf of Mexico at least to the 180 m contour (Leatherwood, Caldwell and Winn 1976). Gunter (1942, 1951, 1954) described aspects of the natural history of bottlenose dolphins along the Texas coast, with emphasis on feeding habits and associations with shrimp boats. Additional work on feeding was reported by Kemp (1949). Copeland (1965) documented the occurrence of bottlenose dolphins in Aransas Pass. Shane (1980) and Shane and Schmidly (1978) investigated numbers, biology, and behavior of a "population" of bottlenose dolphins near Aransas Pass, and Gruber (1981)

made similar detailed observations of bottlenose dolphins near Pass Cavallo. A recent estimate of the number of dolphins in inland waters between Port Aransas and Matagorda, Texas, is 1,319 (Barham, Sweeney, Leatherwood, Beggs and Barham 1980).

MATERIALS AND METHODS

AERIAL SURVEY TECHNIQUES

All aerial observations were made from a high-wing Cessna 172-XP airplane, with one forward and one rear observer positioned on opposite sides. A third individual recorded data. All surveys were flown at an altitude of 150 m and an average ground speed of 167 km/hr, except for brief periods when speed and altitude were reduced for detailed observations of group composition and behavior. Dead reckoning, landmarks, and local navigational aids were used for navigating and estimating the positions of sightings.

When dolphins were sighted, we used hand-held inclinometers or calibrated marks on the wing struts to estimate the vertical angle to the animals, and thereby their right-angle distance from the flight track. This estimation was made while the aircraft was in level flight. The aircraft was generally then diverted from its flight path to circle the animals for identification, enumeration, estimation of relative sizes, and detailed observation of behavior. The aircraft returned to the transect once all data were collected. For all sightings, we noted sighting cues and behavior of the animals at the time of sighting.

Surveys were conducted only when wind and sea surface conditions indicated a Beaufort Index of 3 or below (winds less than about 18–19 km/hr, no more than occasional white foam crests). Adverse weather, which was a factor only once, required suspension of surveys in the Gulf of Mexico with only a partial set of transects completed on 26 September.

AERIAL SURVEY COVERAGE

We planned to follow, with only slight modifications, a survey design employed earlier in Indian River, Florida (Leatherwood 1979) and a region of the southern Texas coast (Barham *et al.* 1980). However, despite apparent physiographic similarities between Laguna Madre and the Indian River, we found that dolphins in the two areas use the environments differently. The near absence of dolphins in Laguna Madre proper and their concentration at the passes connecting the Laguna with the Gulf of Mexico forced us to modify our original survey design and to devote more effort to intensive surveys of the passes and the Gulf side of the barrier islands than we had planned.

In 10 flight days from 21 to 30 September, aerial coverage consisted of: (1) 3 sets of 20 east-west transects in Laguna Madre; (2) 3 north-south flights covering the entire ICW and adjacent waters from the southern end of Corpus Christi Bay to Brownsville Ship Channel (Figs. 1, 2, 3); (3) attempted 100% coverage of Arroyo Colorado (3 times), Aransas Pass (3 times) (Fig. 4), Port Mansfield Pass (7 times) (Fig. 5), and Brazos Santiago Pass (10 times) (Fig. 6), including in the last three cases the ship channels, passes, and adjacent Gulf waters to 3.7 km north and south and 3.7 km directly offshore from the mouths of the passes; (4) 3 sets of randomly-oriented, parallel transects spaced at 1.8 km intervals across the entire width of Corpus Christi and Nueces bays (Fig. 7); and (5) 3 complete sets and one partial set of offshore transects (12–48/day) in a zigzag pattern off the Padre and Mustang island coasts, which covered the Gulf to distances of 2.8 and 8.9 km offshore, essentially to the 180 m contour (Figs. 1, 2, 3).

SHORE STATION SURVEYS

To monitor movements of dolphins between the Laguna and the adjacent Gulf of Mexico and Corpus Christi Bay, shore stations were established at four locations: station 1 at the west passage and station 2 at the east passage of the ICW through John F. Kennedy Causeway (Fig. 1);

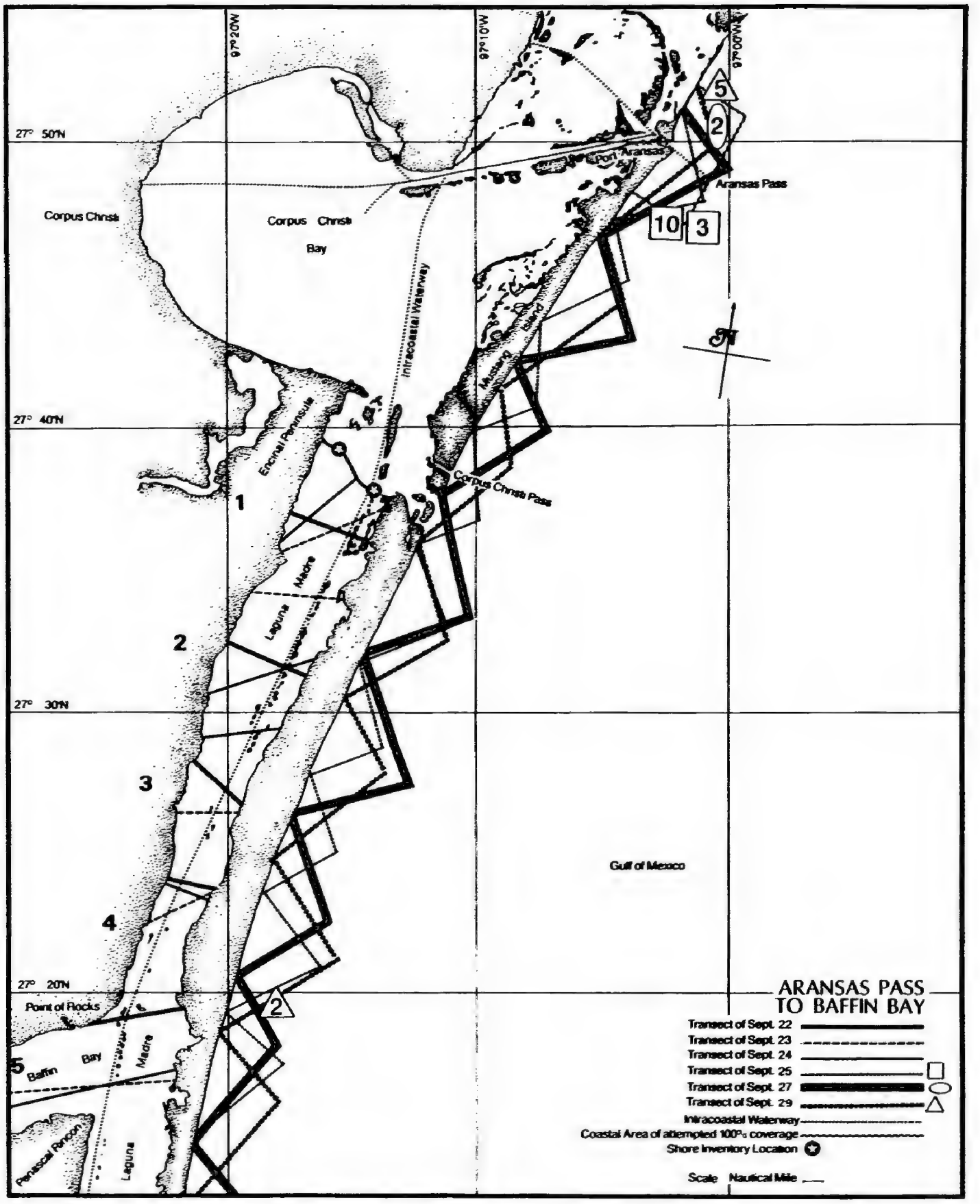

FIG. 1. Inland marine and Gulf coast waters, from Aransas Pass to Baffin Bay, showing placement of transects and locations of sightings of bottlenose dolphins. The numbers in the symbols indicate the estimated number of dolphins.

station 3 on the berm on the north side of Port Mansfield Pass (Figs. 2, 3, 5); and station 4 on a rock-pile on the NW side of Brazos Santiago Pass where it enters Brownsville Ship Channel (Figs. 3, 6). All four shore stations were manned daily from 22 to 27 September (*i.e.*, during the Laguna Madre and ICW surveys) for a total of 203.6 hrs of shore watch.

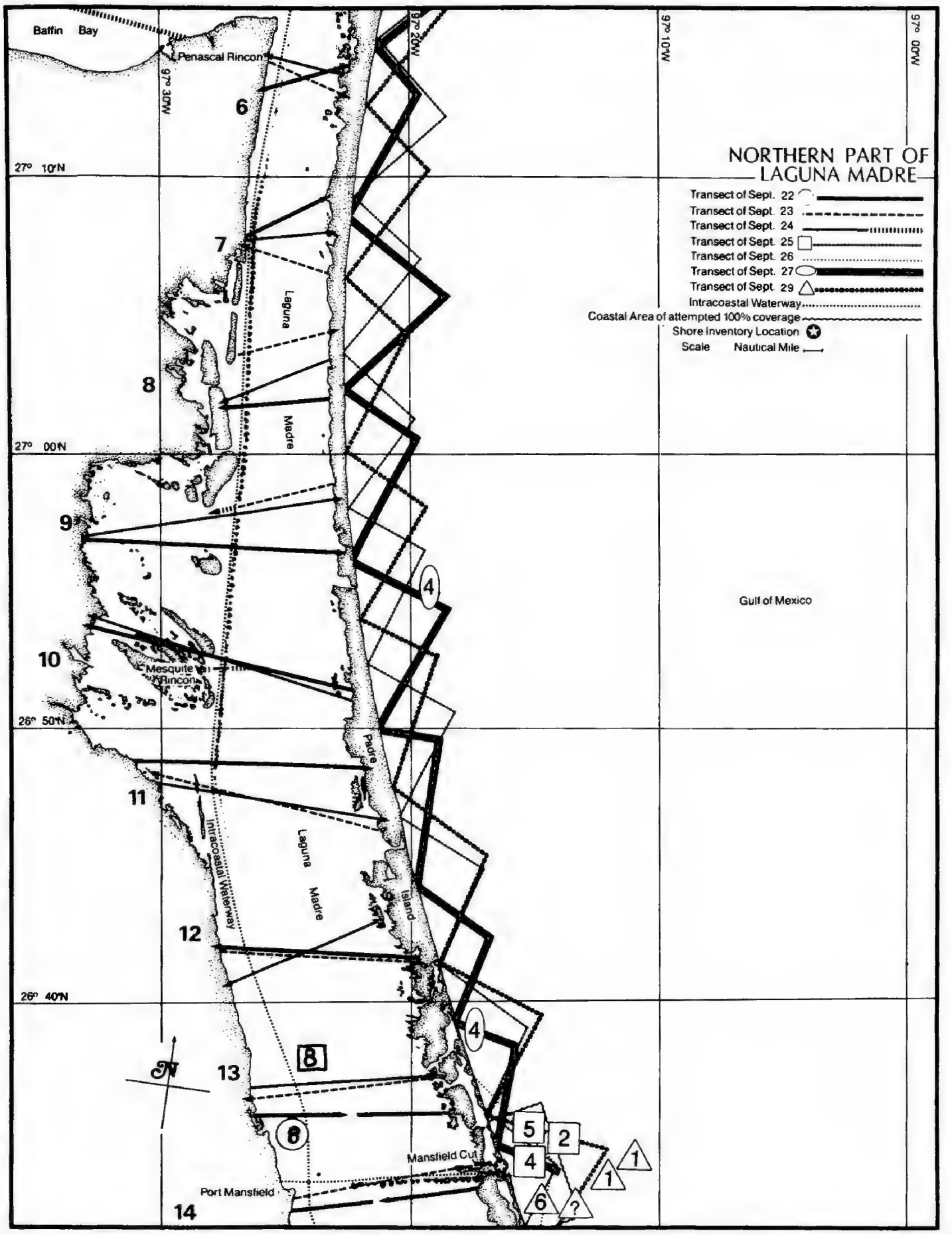

FIG. 2. Inland marine and Gulf coast waters, from Baffin Bay to Port Mansfield and Mansfield Cut, showing placement of transects and locations of sightings of bottlenose dolphins. The numbers in the symbols indicate the estimated number of dolphins.

TREATMENT OF DATA

Distribution of sighting distances from aerial surveys was tested for relative goodness of fit to theoretical models of five line-transect estimators: exponential (Gates, Marshall and Olson

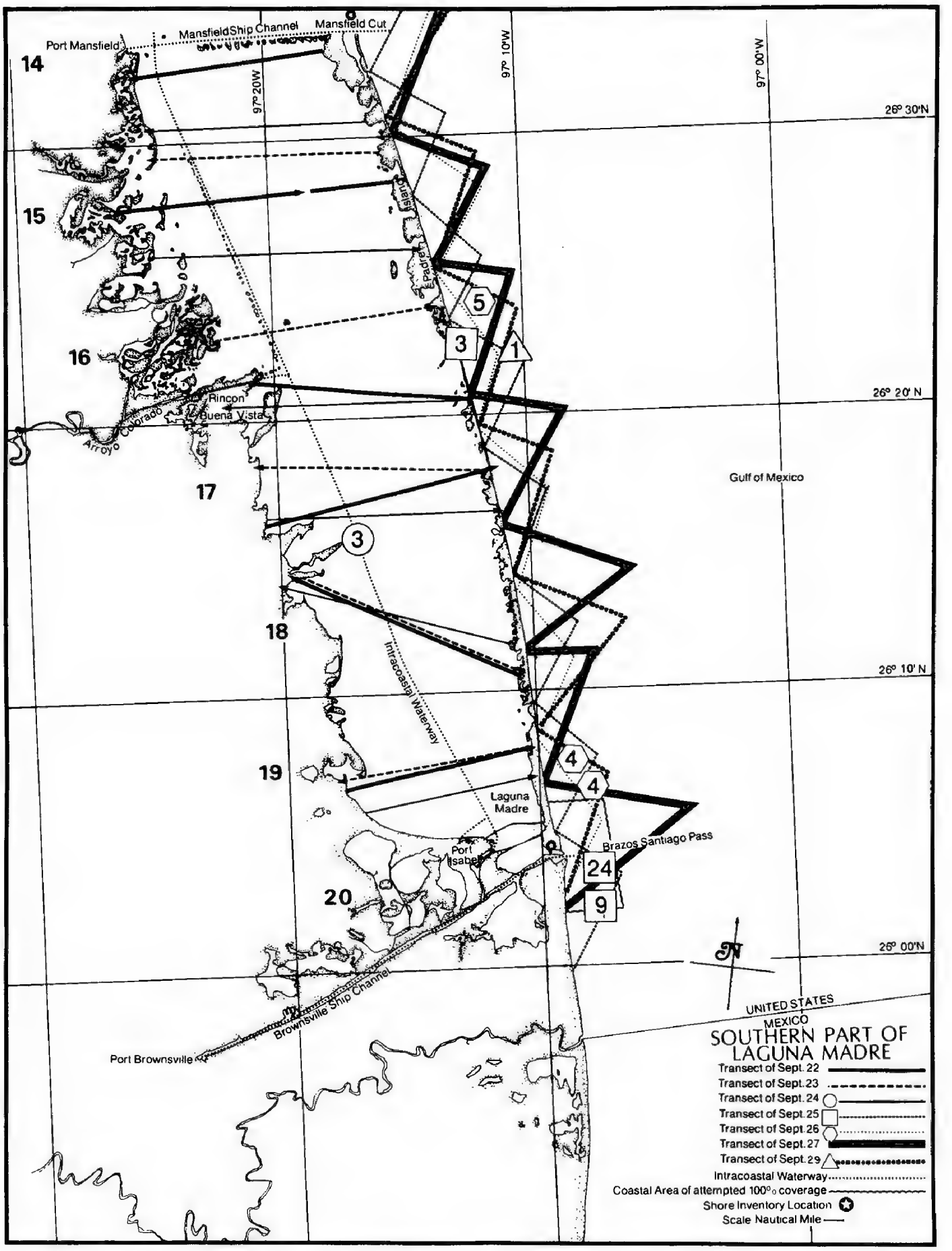

FIG. 3. Inland marine and Gulf coast waters, from Port Mansfield to the United States/Mexico border, showing placement of transects and locations of sightings of bottlenose dolphins.

1968), Burnham-Anderson-Gates nonparametric (Anderson and Pospahala 1970, Burnham and Anderson 1976), Anderson-Pospahala-Parr-Gates (modification of Anderson and Pospahala 1970), half-normal (Hemingway 1971), and Weibull (Pollock 1978, Quinn 1977). The most appropriate model was then applied, following Leatherwood and Show (1980).

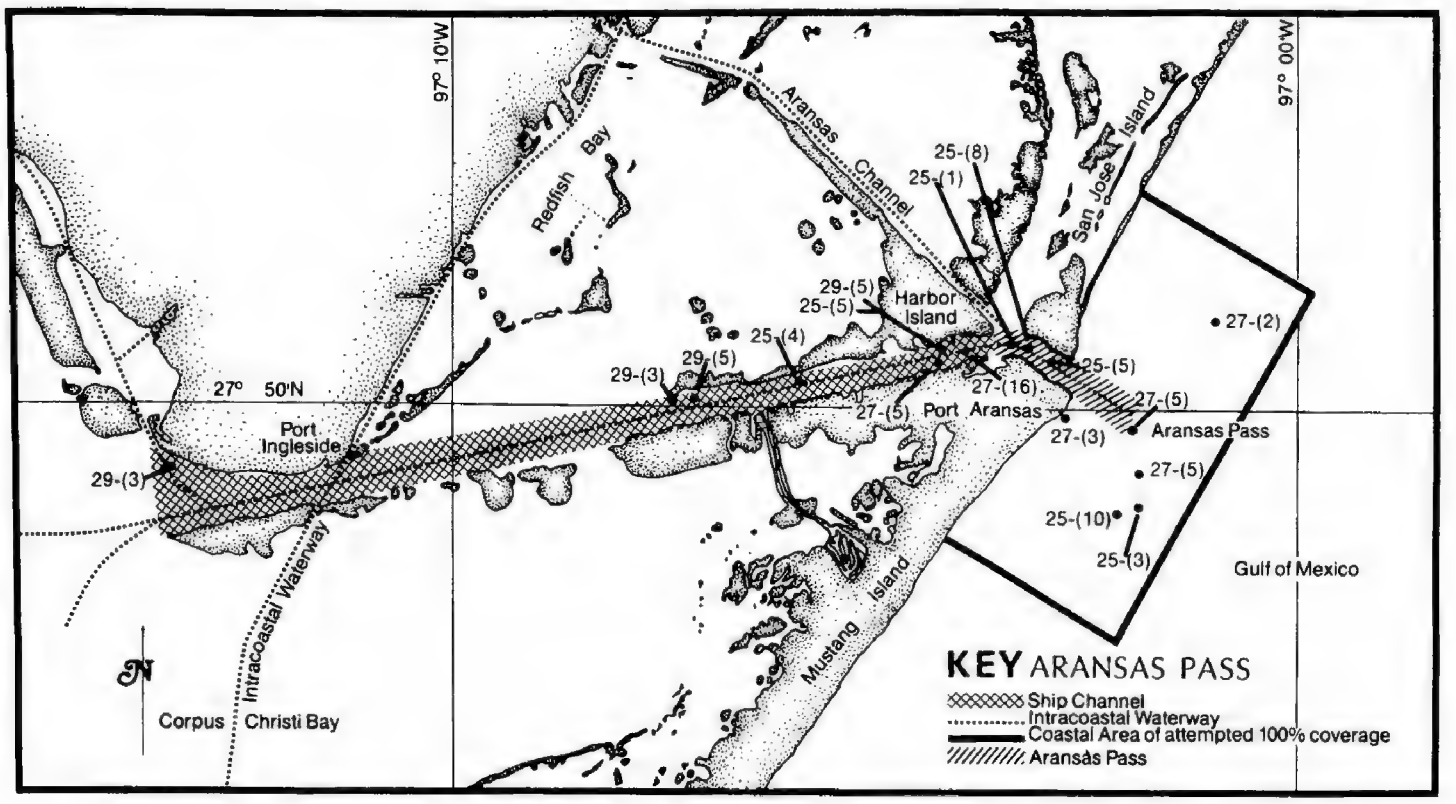

FIG. 4. Detail of Aransas Pass and adjacent Laguna and Gulf of Mexico, showing the locations at which bottlenose dolphins were sighted during attempted 100% counts. The numbers related to the symbols indicate date, survey number for that date (if more than one), and, in parentheses, estimated number of dolphins.

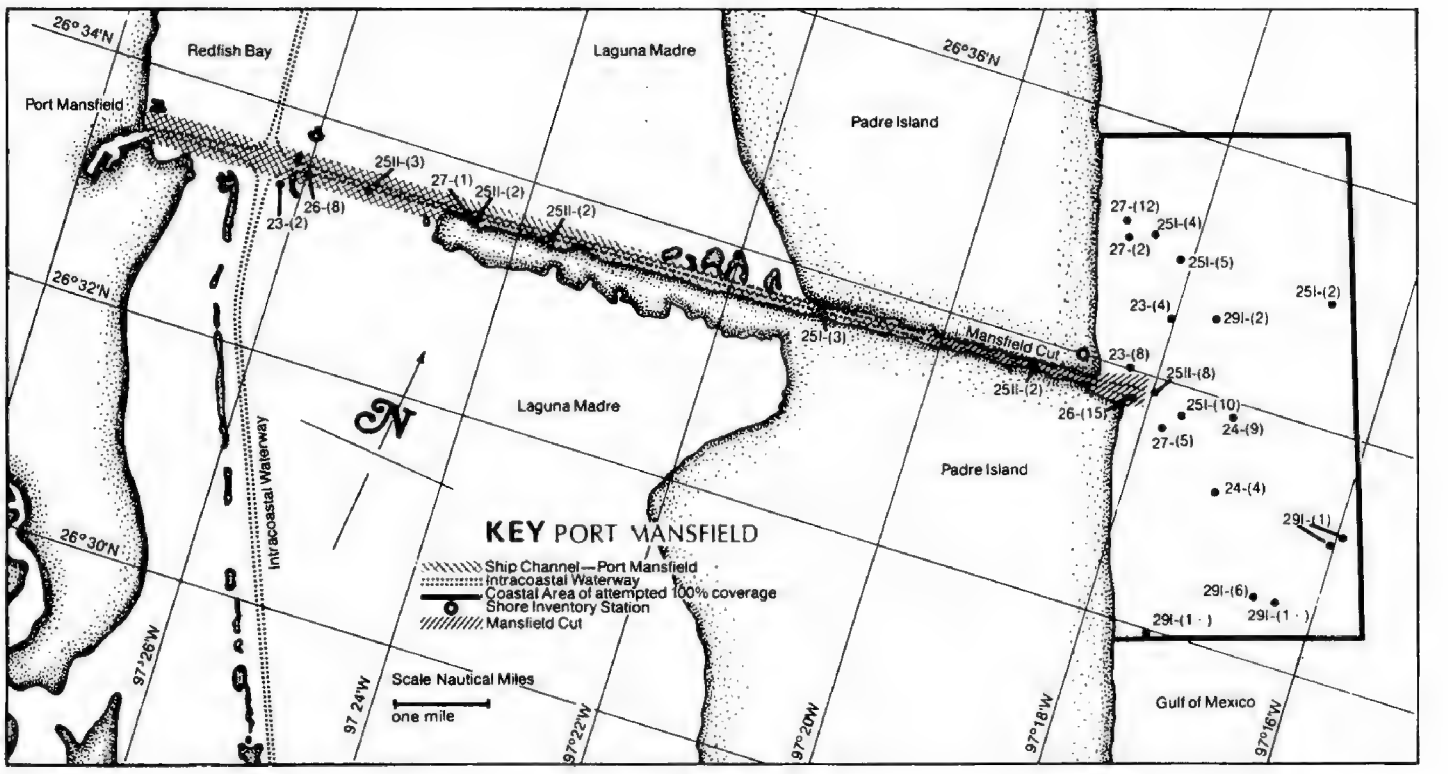

FIG.. 5. Detail of Port Mansfield/Mansfield Cut and adjacent Laguna and Gulf of Mexico, showing the locations at which bottlenose dolphins were sighted during attempted 100% counts. The numbers related to the symbols indicate date, survey number for that date (if more than one), and, in parentheses, estimated number of dolphins.

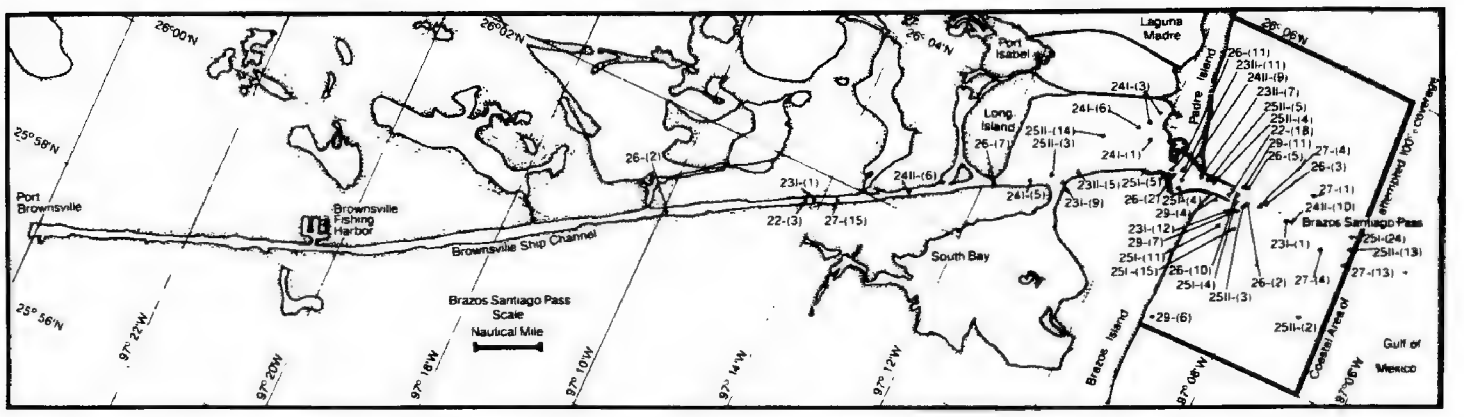

FIG. 6. Detail of Brownsville/Brownsville Ship Channel/Brazos Santiago Pass and adjacent Laguna and Gulf of Mexico, showing the locations at which bottlenose dolphins were sighted during attempted 100% counts. The numbers related to the symbols indicate date, survey number (if more than one), and, in parentheses, estimated number of dolphins.

Population size and density for the flights in the Gulf of Mexico were most appropriately estimated by the Gates estimator (Gates *et al.* 1968), modified to account for the area of obstructed downward visibility along the transect center-line (Leatherwood, Show, Reeves and Wright 1982). The estimator is written in the form:

$$\hat{D} = \frac{n\hat{f}(0)}{2L} \tag{1}$$

where: $\hat{D}$ = estimated herd density,
$\hat{f}(0)$ = the estimated intercept of D,
L = the length of the transects flown, and
n = the total number of herds sighted.

Modification of the estimator results in definition of the new estimate as:

$$\hat{D} = \frac{n\hat{f}(0)}{2L}\left\{[1 - a\hat{f}(0)]^{-1}\right\} \tag{2}$$

where: a is the exclusion area under the aircraft, calculated to be 0.072 km.

The minimum variance of the estimates was calculated, also following Gates *et al.* (1968), by

$$V(\hat{D}) = \frac{\hat{D}^2}{2}\left(Q + \frac{n}{n-2}\right) \tag{3}$$

where: $Q = 1 + \frac{n}{A\hat{D}}$ and A is the area being sampled.

Population size and density for Corpus Christi Bay transects were appropriately estimated following Anderson-Pospahala-Parr-Gates. The estimator is nonparametric; it requires no assumptions concerning the distribution of distance measurements. The estimator is written in the form of equation (1) with $\hat{f}(0) = b_0/w$ and $w = u_2 - u_1$; b_0 is the intercept of a quadratic equation (with $b_1 = \emptyset$) fit to the sighting distance relative frequency distribution, this estimated equation being constrained such that the area under the curve is equal to one. The following empirical variance formula for $\hat{D}$ is used:

$$V(\hat{D}) = C^2\left\{n^2V[\hat{f}(0)] + [(\hat{f}(0)]^2V(n) - V[\hat{f}(0)]V(n)\right\} \tag{4}$$

where: $C = 1/2L$

This expression assumes that n and $\hat{f}(0)$ are independent, a reasonable biological assumption. The value of $V[\hat{f}(0)]$ is estimated by first calculating $S_{y\cdot x}$, the mean square deviation from the fitted quadratic equation. Then $V[\hat{f}(0)]$ is estimated as the usual variance of the intercept

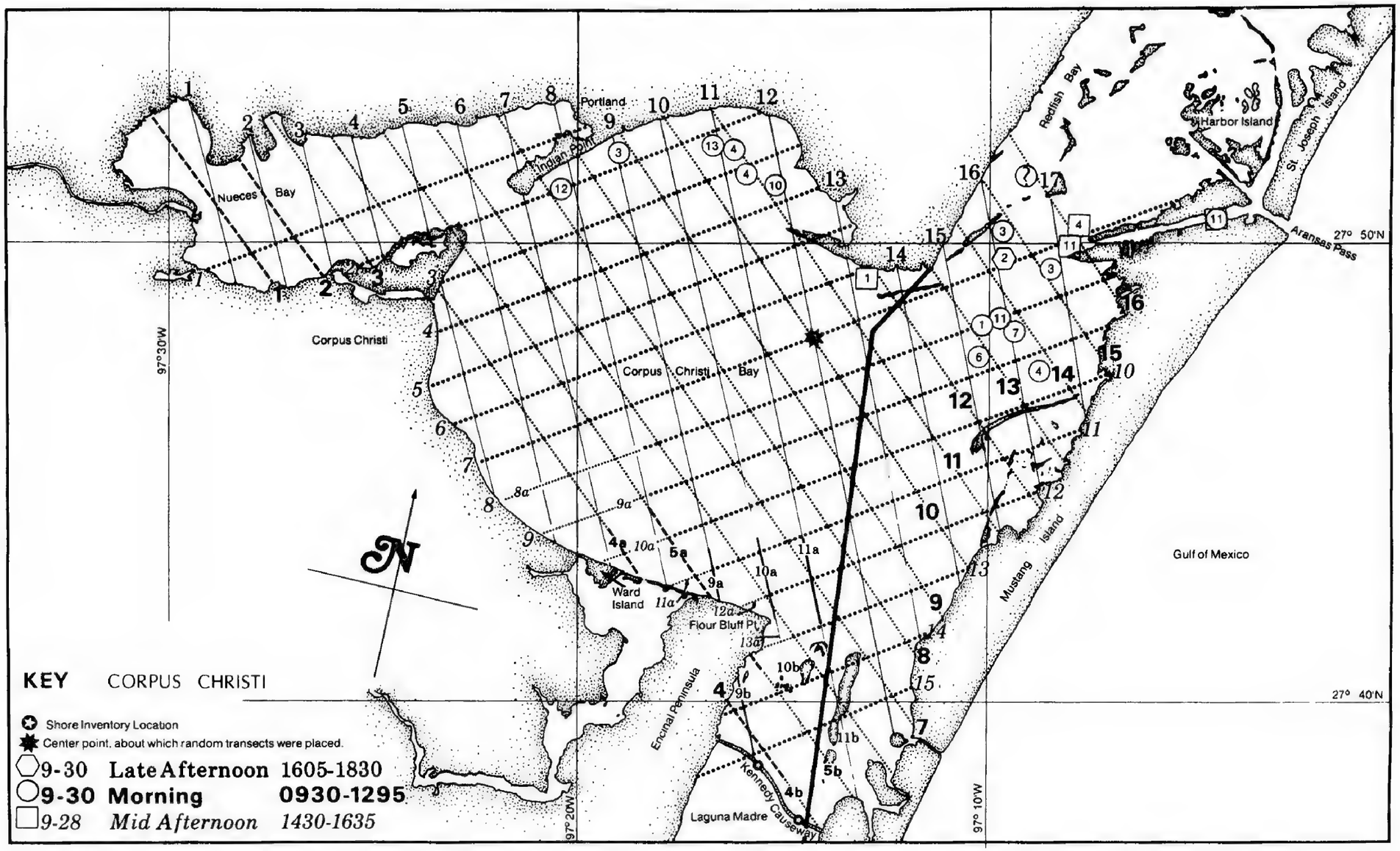

FIG. 7. Corpus Christi Bay and Nueces Bay, Texas, showing the placement of radial transects and the locations at which bottlenose dolphins were sighted. The numbers in the symbols indicate the estimated number of dolphins.

$$V[\hat{f}(0)] = S^2_{y.x}\ C_{00} \qquad (5)$$

where: c_{00} is the appropriate element of the $(x'x)^{-1}$ matrix, $(x'x)$ being the product-cross product matrix.

RESULTS

LAGUNA MADRE TRANSECTS

Transects in Laguna Madre (Figs. 1, 2, 3) covered a total of 527.6 linear km, about 37.6% of which was over what we considered acceptable habitat for bottlenose dolphins, *i.e.* water more than about 0.2 m deep at mean low tide and not completely enclosed by shallower areas that prevented ingress and egress by dolphins. All surveys were flown under nearly ideal conditions of Beaufort 2 or less; most were flown over clear water (70%) or over areas with some visibility through the water (19.25%). Nevertheless, there was only one sighting in Laguna Madre proper, which consisted of 8 animals in the ICW just north of Port Mansfield Ship Channel on 22 September (Fig. 2).

INTRACOASTAL WATERWAY (ICW) SURVEYS

The ICW surveys covered some 555 linear km and an estimated 513 km^2. Sighting conditions were excellent; so we were confident that if dolphins had been present in substantial numbers, we would have seen them. However, only two groups were seen: one with 3 animals just north of Port Isabel on 24 September (Fig. 3) and a group of 8 just north of Port Mansfield on 25 September (Fig. 2).

Too few sightings were made on the Laguna and ICW transects to make a meaningful estimate of density. The infrequency of observations suggests that dolphins were rare in the Laguna and made little use of the ICW during the survey period. The few animals seen were near the ship channels and passes.

SHORE STATION SURVEYS

No dolphins were reported near stations 1 and 2 despite excellent visibility at both sites for the entire 6 days. Since the ICW is a 38-m wide channel at both passages, which are clearly demarcated and easily monitored, it is unlikely that dolphins could have moved past either station unnoticed. Personnel manning the bridge maintenance facility near station 1 recounted that a single dolphin was seen to pass under the bridge on 18 September, an event they considered uncommon.

A total of 24 groups consisting of 62 individual dolphins was seen at station 3. Most dolphins (13 of 16) were moving with the tidal flow. The net difference in movement among animals entering and leaving the Laguna favored emigration.

A total of 52 groups and 189 individuals was seen at station 4. There was little difference in numbers of animals swimming with (21) and against (17) tides. Again, net movement favored emigration.

Except for the first two days at station 3, counts were similar among days. The low counts on those earlier days may reflect observer inexperience and time spent relocating camps, rather than real differences in the number of animals present. Observers at stations 3 and 4 noted individual dolphins with natural marks sufficiently distinctive to allow re-identification in successive encounters. Repeated sightings of naturally marked individuals and consistency of counts suggest that animals remained near the passes, but entered and left the Laguna periodically.

ATTEMPTED 100% COUNTS

No dolphins were seen in Arroyo Colorado during three 25-minute surveys of that waterway. Because of its narrowness (38 m wide), shallowness (2.75 m deep), water clarity (bottom visible in about 30%, and good visibility through the water in 60%, of the area), and good surface conditions (Beaufort 0 or 1), it is likely that any dolphins present would have been detected.

Counts of 16–36 ($\bar{x}$ = 29.3), 12–24 ($\bar{x}$ = 17.7), and 18–63 ($\bar{x}$ = 32.4) dolphins were made at Aransas, Port Mansfield, and Brownsville, respectively (Table 1). Aerial counts in each pass were consistent among days. Furthermore, aerial and shore counts at the two southern passes were not significantly different statistically (t-test, α = 0.05) (Table 2). Sightings of dolphins in the open Gulf made during times at 100% counts dropped off significantly with distance away from the mouths of the passes.

CORPUS CHRISTI BAY SURVEYS

All surveys in this area were conducted under excellent conditions—Beaufort 3 or less, visibility 3.7 km or greater. Ninety-one percent of the effort covered open bay water; the remainder intersected dredged ship channels.

The 3 sets of transects resulted in 21 sightings, including 17 on transect and 4 off, the latter made while circling and therefore not included in the density estimates. Perpendicular sighting distance was recorded for 13 of the 17 on-track sightings; it ranged from 0.19 to 0.86 km ($\bar{x}$ = 0.48 km).

All sightings were in the north and east portions of the bay, in or near Aransas Ship Channel or the contiguous ICW. Despite intensive coverage of the open bay south of the Aransas area, much of it under optimal survey conditions, no dolphins were seen there. The 38 sightings (all days) for which group size was determined included 1 to 20 individuals ($\bar{x}$ = 6.10) (Figure 8). Calves comprised 4.4–5.6% of all animals seen (Table 3).

GULF OF MEXICO SURVEYS

The 4 sets of transects resulted in 18 sightings on track and 4 off. Perpendicular sighting distance (14 recorded) ranged from 0.09 to 1.74 km ($\bar{x}$ = 0.54 km). If the two longest distances (1.63 and 1.74 km) are discarded as outliers, the mean is substantially reduced ($\bar{x}$ = 0.35 km). In the 39

TABLE 1

Results of attempted 100% aerial counts of bottlenose dolphins in Aransas Pass, Mansfield Cut (Station 3), and Brazos Santiago Pass (Station 4), including in each case the adjacent Gulf (A), pass (B), and ship channel (C).

				#	Total # Animals			
		Date	Time	Sightings	A	B	C	All
ARANSAS	PASS	25 Sept.	1330-1345	7	13	0	23	36
		27 Sept.	0810-0840	6	15	0	21	36
		29 Sept.	0855-0915	4	0	0	16	16
		Means	----	5.7	9.3	0	20.0	29.3
MANSFIELD	CUT	23 Sept.	1524-1553	3	12	-	2	14
		24 Sept.	1016-1042	2	13	-	-	13
		25 Sept.	1053-1114	5	21	-	3	24
		25 Sept.	1635-1700	5	8	2	7	17
		26 Sept.	1045-1105	2	15	-	8	23
		27 Sept.	1037-1101	4	19	-	1	21
		29 Sept.	1137-1157	5	>12	-	0	12
		Means	----	3.7	>14.3	0.3	3.0	17.7
BRAZOS SANTIAGO	PASS	22 Sept.	1415-1444	2	-	18	12	21
		23 Sept.	0806-0844	4	13	-	10	23
		23 Sept.	1624-1647	3	-	18	5	23
		24 Sept.	0859-0935	5	-	-	18	18
		24 Sept.	1641-1702	3	10	9	6	25
		25 Sept.	0912-0941	6	54	9	-	63
		25 Sept.	1723-1754	7	18	9	17	44
		26 Sept.	0857-0945	10	5	28	9	42
		27 Sept.	1532-1539	5	22	-	15	37
		29 Sept.	1236-1259	4	28	-	-	28
		Means	----	4.9	15.0	9.1	9.2	32.4

sightings for which group size was determined there were 1 to 24 dolphins ($\bar{x}$ = 5.23) (Fig. 9). Calves comprised 6.1% of all animals seen (Table 3).

CALCULATION OF DENSITY ESTIMATES

In order to calculate density estimates (with variances) we require: (1) an estimate of area effectively surveyed; (2) the total area to which the

TABLE 2

Comparisons of counts of bottlenose dolphins from aircraft and shore stations at Port Mansfield (Station 3) and Brazos Santiago Pass (Station 4). Note that aerial counts represent the number of different dolphins seen in 20–29 min (Mansfield) and 7–48 min (Brazos Santiago) periods of observation, while shore counts are estimated total numbers of different dolphins seen from the shore station during periods of observation lasting from 4 hr 35 min to 11 hr 15 min (Station 3) and 7 hr 15 min to 10 hr 39 min (Station 4).

Date	Station 3 (Mansfield) Aircraft	Station 3 (Mansfield) Shore	Station 4 (Brazos Santiago) Aircraft	Station 4 (Brazos Santiago) Shore
22 Sept.	-	3	21	31
23 Sept.	14	5	23	34
23 Sept.	-	-	23	-
24 Sept.	13	21	18	35
24 Sept.	-	-	25	-
25 Sept.	24	10	63	40
25 Sept.	17	-	44	-
26 Sept.	23	10	42	32
27 Sept.	21	13	37	17
29 Sept.	12	-	28	-
Totals	124	62	324	189
$\bar{X}$	17.7	10.3	32.4	31.5

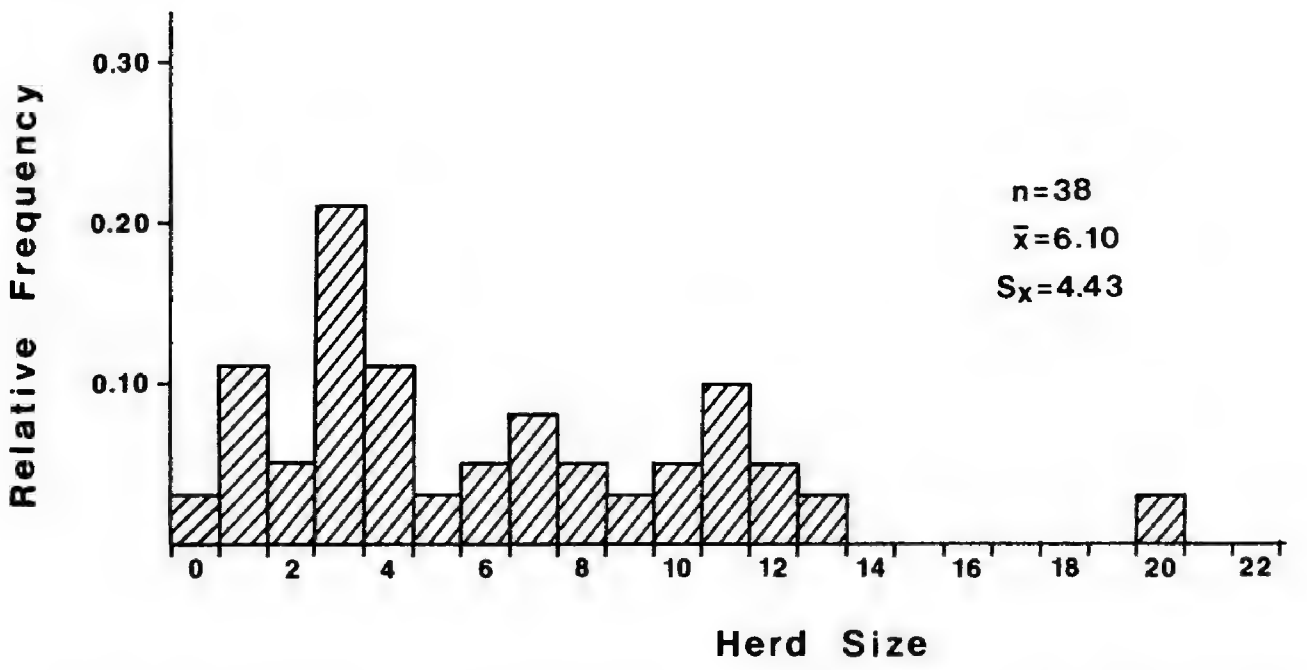

FIG. 8. Distribution of dolphin herd sizes from Corpus Christi Bay aerial surveys.

TABLE 3

Numbers of bottlenose dolphins classified as calves, from aerial observations.

	Total # of Animals	# of Calves	% of Total
Aerial Observations Gulf of Mexico Systematic Transects	99	6	6.06
Seaward of Cut (100% counts)			
Brownsville	155	10	6.45
Pt. Mansfield	102	12	11.76
Aransas Pass	32	1	3.12
Inside Cuts			
Brownsville	91	1–3	1.10–3.30
Pt. Mansfield	2	0	0
Aransas Pass	0	0	0
In Ship Channels			
Brownsville	83	8	9.64
Pt. Mansfield	21	1	4.76
Aransas Pass	98	10	10.20
Corpus Christi Bay	90	4–5	4.44–5.55
Laguna Madre (on random transects and ICW surveys)	19	2	10.53
TOTALS	792	50–55	6.31–6.94

estimates will be extrapolated; and (3) the number of animals per herd. The area effectively surveyed can be estimated for transects with nonoverlapping coverage by:

$$A = L \times (W \times 2) \qquad (8)$$

where: A = area,
L = total distance flown, in linear km, and
W = effective sighting distance (one-half effective strip width);

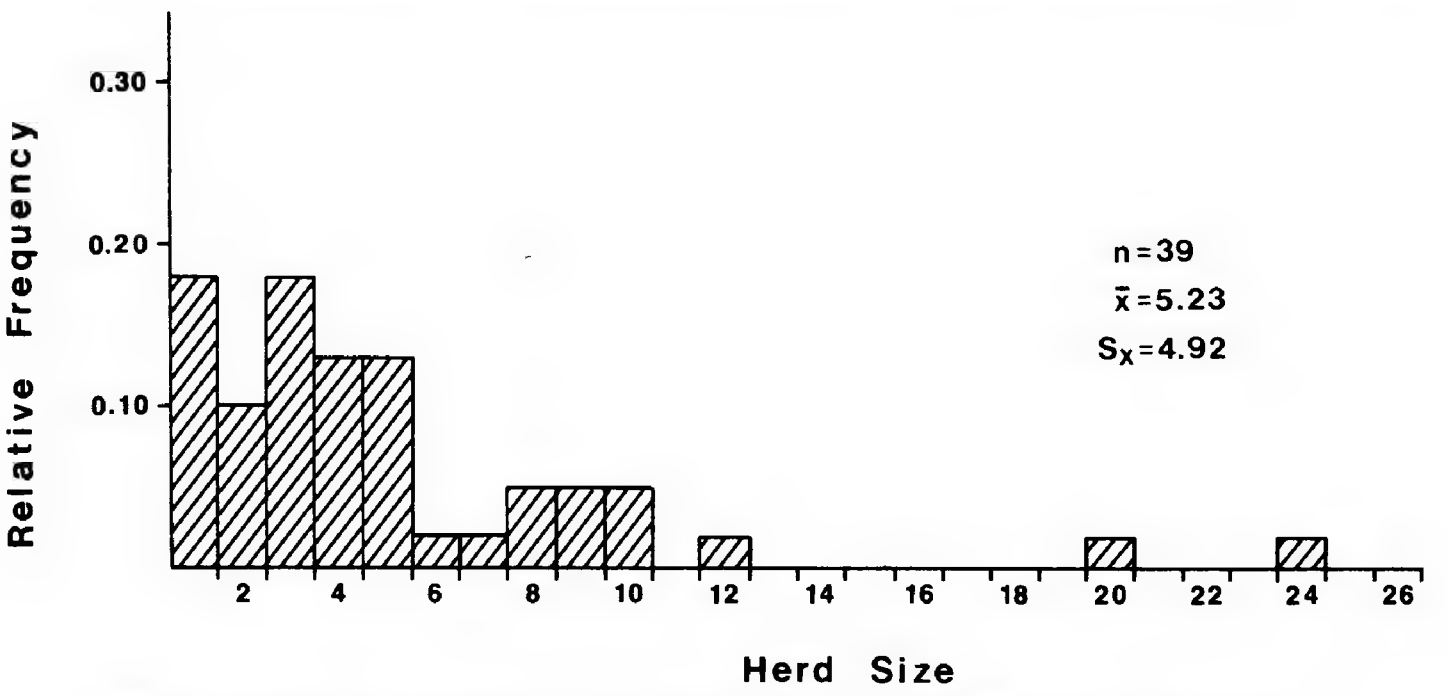

FIG. 9. Distribution of dolphin herd sizes from Gulf of Mexico aerial surveys.

or for transects with areas of overlapping coverage where transects are at right angles to each other, by:

$$A = L \times (W \times 2) - \frac{1}{4}[(T-1) \times W^2] \qquad (9)$$

where: T = the number of contiguous transects on which there is overlapping coverage.

The density of sightings can then be estimated, following Gates *et al.* (1968), by:

$$\hat{D} = \frac{(n - 1)}{A} \qquad (10)$$

where: n = number of herds sighted, as in equations 1 and 2.

The area effectively surveyed was determined by doubling the effective one-sided strip width (w), estimated independently for the two areas by using all sightings on transect (with the exception of the two most distant sightings in the Gulf surveys, which were discarded). The value of w was calculated as 0.22 km for the Gulf and 0.28 for Corpus Christi Bay. A planimeter was used on a detailed hydrographic chart to estimate total area to which density estimates were to be extrapolated.

Herd densities ($\hat{D}_h$) were calculated by the method of Gates *et al.* (1968) (see equations 1 and 2). Then population densities ($\hat{D}$) were calculated by:

$$\hat{D} = \hat{D}_h \bar{H} \qquad (11)$$

where: $\bar{H}$ = mean herd size.

This calculation assumes only that sightings of herds are independent of one another. No such assumption is made concerning associations of individuals within herds.

The variance of $\hat{D}_h$ is calculated following Gates *et al.* (1968), equation 3. The variance of $\hat{D}$ is calculated, following Leatherwood *et al.* (1978), by:

$$V(D) = \bar{H}^2 V(\hat{D}_h) + \hat{D}_h^2 V(\bar{H}) - V(\hat{D}_h)V(\bar{H}). \qquad (12)$$

We estimate 0.168 dolphin herds/km² in Corpus Christi Bay and 0.06 herds/km² in the nearshore Gulf of Mexico between shore and the 18 m contour off Padre and Mustang islands (Table 4).

TABLE 4

Estimates of herd density and total population size for bottlenose dolphins in Corpus Christi Bay (above) and the Gulf of Mexico (shore to the 18 m contour) off Padre and Mustang islands (below), with 95% confidence limits and variances of the mean population estimates. Corpus Christi Bay estimate used Anderson-Pospahala-Parr-Gates estimator; Gulf of Mexico, Gates estimator.

CORPUS CHRISTI BAY

Date	L(km)	A(km^2)	Herd Density (herds/km^2)	Estimated Total Population Size
28 Sept.	227.6	101.1	0.104	64
30 Sept.	251.4	101.1	0.376	232
30 Sept.	245.3	101.1	0.024	14.8
Mean	241.4	101.1	0.168	103.4

$\bar{H}$ = 6.10 CL = [67.3, 139.5] V = 12902.5

GULF OF MEXICO

Date	L(km)	A(km^2)	Herd Density (herds/km^2)	Estimated Total Population Size
25 Sept.	295.1	956.5	0.071	353.3
26 Sept.	76.4	956.5	0.078	389.4
27 Sept.	318.6	956.5	0.019	95.0
29 Sept.	287.7	956.5	0.073	364.5
Mean	244.5	956.5	0.060	300.5

$\bar{H}$ = 5.23 CL = [226.6, 374.4] V = 19238.2

DISCUSSION AND CONCLUSIONS

Estimates of density in Corpus Christi Bay are lower than those from the nearby Aransas Pass/Matagorda region (Barham *et al.* 1980). Numbers estimated in the present study depended largely on sightings made near Aransas Pass rather than in the bay itself. During several reconnaissance flights into the northern end of Corpus Christi Bay in April 1978, E. G. Barham (personal communication) found no dolphins, despite large concentrations in all the channels of Aransas Pass. Interviews with knowledgeable local mariners at Aransas Pass, Rockport, and Matagorda in March 1978 and with biologists at Corpus Christi and Aransas Pass in September 1979, strongly suggested to us that dolphins, once present in substantial numbers in Corpus Christi Bay, had become far less common in recent decades. We know of two recent records of dolphins in the southern end of the bay near the time of our study—the single animal passing through the western branch of the ICW at John F. Kennedy Causeway on 18 September (see above) and two animals seen off the southwest arm of the ship channel near the Naval Air Station, Corpus Christi, on 24 September (B. Chapman, personal communication). Though we were informed by several local biologists that dolphins use the entire bay system, we did not see them anywhere in the bay except in or near Aransas Pass, the contiguous arms of the ICW, and other ship channels.

There is no consensus among statisticians about which methods are appropriate for estimating dolphin population size from aerial survey data (Chapman 1982), particularly from aircraft with obstructed downward visibility (Thompson 1981). Therefore, we welcome recalculations of numbers from the data presented here once an agreed-upon model is available. Regardless of the analytical methods applied, however, we urge that results of aerial surveys such as those reported here be interpreted with caution because of the short period they represent. Shane's (1977, 1980) peak census total occurred in January, and her lowest population numbers were for October. Therefore, we may have been surveying at a season when the local population is well below its annual peak.

The estimated density of dolphins in the Gulf of Mexico (0.314/km^2) was considerably lower than that reported to date for any other open-water area of the Gulf of Mexico (Leatherwood and Reeves 1982). We have no explanation for the apparently low density, and there are no previous estimates from the Texas Gulf coast with which to compare them. Gunter (1954) reported that the population off Texas had declined considerably, but he gave no quantitative basis for this assertion. His statement raises the interesting question of whether redistribution of animals rather than a decrease in population size might account for apparent changes in abundance in certain areas.

Like Barham *et al.* (1980), we found that animals in the Gulf were concentrated near the mouths of the major passes. There were far fewer sightings between Port Mansfield Cut and Aransas Pass than there were in

the shorter segment between Port Mansfield Cut and Brazos Santiago Pass. Similarly, the only observations of dolphins in Laguna Madre were near the inner arms of those cuts and related ship channels. Gunter's (1967) statement that the bottlenose dolphin "is not found in the Laguna Madre" is not strictly true at present. They have been seen in Arroyo Colorado and in the shallow waters adjacent to Port Isabel (J. Breuer, personal communication), in the ICW 30 km north of Port Mansfield, at the entrance to the land-cut (R. Bennett, personal communication), and in Baffin Bay (S. Cornelius, personal communication). However, dolphins do not appear to be common in any of these areas. There seems to be wide agreement that the bulk of the dolphin population has a limited distribution centering in and near the passes. Such non-uniform distribution is an important consideration in population estimation; it also has interesting ecological implications. Most of our informants believed there to be a causal relationship between shrimp fishing and other human activities at the passes, and the tendency of dolphins to concentrate there. This would be consistent with observations made in other areas (see Leatherwood 1975, for a review). Near Matagorda, Texas, less than 185 km from the Laguna Madre area, bottlenose dolphins apparently have adjusted their feeding strategies and distribution at certain seasons to shrimping activities (Gruber 1981).

Corpus Christi and Nueces bays together cover some 150 km^2, of which we estimate about 101 km^2 to be acceptable habitat for dolphins. Our population estimate for that area is 103.4 (67.3, 139.5). The open Gulf from immediately north of Aransas Pass to immediately south of Brazos Santiago Pass, and seaward to approximately the 18 m contour, includes an estimated 956.5 km^2, all of which we consider suitable dolphin habitat. Our estimate for this portion of the Gulf is 300.5 (226.6, 374.4) dolphins. It must be remembered that these estimates extrapolate the density estimates to the total area judged acceptable, while in reality the dolphins were recorded more frequently in and near the ICW or the passes. If adequate data become available for these and other areas, weighted treatments of probability of use of each area by dolphins should be routinely figured into estimates of population size from observed densities.

Mean counts of dolphins at the three major passes were 29.3, 17.7, and 32.4, north to south. The extent to which the animals counted at the passes are also included in estimates for the Bay and the Gulf is unknown, but if these figues are considered non-redundant and added to upper and lower confidence limits of the previous two estimates, the estimate of dolphin abundance in all the areas surveyed is 373.3 to 593.3 animals. Our subjective impression is that these figures are realistic. There certainly were less than thousands and more than tens of animals in the study area at the time of these surveys.

The 6.3 to 6.9% calves observed during this study is well within ranges reported elsewhere for the species (see Leatherwood and Reeves 1982, Table 18.1). Contributors to Ridgway and Benirschke (1977) presented strong evidence for spring and autumn peaks in calving for bottlenose

dolphins, and Leatherwood (1977) suggested average annual calf production to be as high as 11.4 to 12.4%. The percentage of calves observed during this study may be relatively low because many of the animals were approaching the end of their first year (by which time they are close to 2 m long) and were not recognized and scored as calves.

Human manipulation of the environment often works to the disadvantage of other life-forms. The bottlenose dolphin, like the white-tailed deer *(Odocoileus virginianus),* may be an exception to this pattern, at least in portions of southern Texas. Here the "land-cut" north of Port Mansfield allows dolphins to move freely between Corpus Christi and the Port Mansfield area. Although there is little evidence that they avail themselves of this stretch of the ICW on a regular basis, there is considerable evidence that dolphins use intensively and regularly the artificially maintained passes at Port Mansfield and Port Isabel, as well as their associated ship channels. The creation and maintenance of navigable passes and the resultant reduction in lagoon salinity may have created "new" habitat for dolphins. Such habitat changes could possibly modify dolphin distribution and/or cause a change in their population size. Several long-term residents of the area told us that populations of sport fish like black drum *(Pogonias cromis)* and redfish *(Sciaenops ocellatus),* and "trash" fish like mullet *(Mugil* sp.), in Baffin Bay and elsewhere in Laguna Madre have benefited from the relatively stable salinity regime created by the dredging projects. Mullet and black drum are known prey of bottlenose dolphins (Gunter 1942, Leatherwood 1975). It was our impression that dolphins were feeding actively in the ICW, the ship channels, and the cuts; in fact, they appeared to prefer the muddy, turbulent zones at the entrance to cuts and along the margins of dredged channels. So few dolphins in the Laguna proper, despite the visible presence of large concentrations of fish in many parts of it, was surprising.

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